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by

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and

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NATURE CONSERVATION AND NATURE RESERVES

Report of the Committee appointed by Council on 26 May 1942

Approved by Council, October 1943*

Revised Terms of References (5 January 1943). To consider and report on the whole question of the conservation of nature in Britain with special reference to plant and animal communities and species, and to draw up a list of areas that should, on ecological grounds, be kept as National Nature Reserves.

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INTRODUCTORY NOTE. THE N.R.I.C. REPORT

Your Committee have found themselves in some difficulty because of the co-existence of the 'Nature Reserves Investigation Committee' with very similar terms of reference. That Committee was appointed in the Summer of 1942, shortly after the appointment of our own Committee, by the Conference on Nature Preservation in Post-War Reconstruction, which was itself formed in 1941, on the invitation of the Society for the Promotion of Nature Reserves, of delegates from societies and other bodies interested in natural history. The Conference held three meetings during 1941 and laid down certain principles concerning nature conservation and the selection, use and maintenance of Nature Reserves (Conference Memorandum No. 1, November 1941). In 1942 Sir William Jowitt, in his capacity as chairman of the Ministerial Committee concerned with problems of reconstruction, invited the Conference to appoint an appropriate Committee which could advise Government on matters relating to Nature Reserves. The Conference forthwith appointed the N.R.I.C.

It will thus be seen that the N.R.I.C. is a quasi-official body, and it has facilities for carrying out its work which are far greater than those available to the British Ecological Society. Furthermore, the interests of ecology are well represented on the N.R.I.C. by several prominent members of the B.E.S., though they serve as appointees of the Conference, not as directly representing the B.E.S. It might therefore be held that the work of the B.E.S. Committee was unnecessary and redundant. That, however, was not the view taken by our Council, nor by at least two of our members who are also members of the N.R.I.C. It is felt that the interests of ecology as such and the views of ecologists ought to be independently formulated, and that our Society is the proper agency to do this and to draw up a list of areas which should be preserved as of national importance on ecological grounds. But it is also true that the motives for nature preservation which are not specific to ecological science are so mixed with those which are that it becomes misleading to deal with the latter alone and to omit all reference to the former.

For these reasons the Committee asked for a revision of its original terms of reference, and those

* This Report has also been published in the *Journal of Ecology*, vol. 32, pp. 45–82, 1944, and reprints can be bought from the Cambridge University Press, for 1*s*. 6*d*. each.

quoted at the head of this Report have been adopted by Council. The following Report, therefore, while naturally written from the ecological point of view, attempts to argue the case on the widest grounds and to make suggestions in other interests besides those of specialized ecology. Considerable use has been made of the memoranda and report* of the N.R.I.C.

Two important conclusions which have necessarily affected the work of your Committee have been reached by the N.R.I.C. One is the decision to separate *National Reserves* from *Local Reserves*, the former to represent a minimum of habitats and communities which should be preserved as of national importance and which it is recommended should be acquired outright by the State; while the latter, many of which already exist, would be preserved in other ways by various bodies or persons, including Local Authorities, and administered locally. The other decision is to form local committees, eventually to cover the whole country, for the purpose of obtaining adequate information as to areas it is desired to preserve. The chairman of the B.E.S. Committee independently came to the conclusion that this is the only effective means of obtaining the necessary data. The data obtained directly by the B.E.S. Committee have therefore been sent to the appropriate local sub-Committees of the N.R.I.C. to assist them in their work.

A list of habitats, with their types of vegetation, which should be represented among National Reserves and a list of suggested National Reserves have been prepared and transmitted to the N.R.I.C. for their information.

The Committee expresses its debt to Mr Charles Elton, Mr H. N. Southern and Dr E. B. Worthington, who supplied valuable memoranda on which the sections dealing with the conservation of animals are mainly based; and to Dr A. S. Watt and Dr A. R. Clapham in regard to Forestry.

1. WHAT IS THERE LEFT TO PRESERVE? VEGETATION AND ANIMAL LIFE OF GREAT BRITAIN

Though the face of Great Britain has been greatly changed by man's work through the centuries, so that most of it is farmland while large parts are now built over, yet there do remain considerable tracts of wild vegetation, much more extensive of course in the wetter climates of the west and the bleaker conditions of the north, where the soils also are on the whole less fertile and less suitable for farming. As the human population has increased in density the populations of larger wild animals have naturally been greatly reduced. Not only have the larger carnivorous mammals been exterminated and the larger predatory birds greatly lessened in numbers, but various other species have decreased or disappeared as suitable habitats became more and more restricted. Nevertheless, the bird population is large, comprising several hundred species, and there are quite a number of small mammals, largely rodents, some of which are too numerous. Of invertebrate animals there are vast numbers of species and individuals belonging to many different groups, though the butterflies and moths are almost the only ones that attract much popular interest.

The wild life of our country is part of our national heritage. Together with and determined by the climate, the physical features and the varied soils, the natural vegetation of the country, with the animals which haunt it, forms the original scene in which our history has unfolded and has largely conditioned the development of our culture and civilization. It has always been and still is a vital source of conscious pleasure and refreshment to large sections of the population, and unconsciously at least it is part of the breath of life of every countryman. To-day it demands our conscious and alert attention, for in the inevitable changes of the next few decades much of what remains will be seriously threatened with destruction or degradation even more rapid than in the recent past. We must preserve what we can of this precious and beautiful heritage, just as we preserve what we can of our ancient buildings and monuments, largely for the same reasons, but also for others.

We cannot of course preserve the whole of what remains. The claims of new building, of agriculture and forestry, must take a prominent place in post-war development. And some animals are too numerous for human welfare. What we can do is to survey the whole problem with careful attention and then take steps to conserve, under proper control, more or less extensive samples of our natural vegetation and so much of our wild animal life as is reasonable and practicable, for our mental refreshment, for the enjoyment of its beauty and interest, and for purposes of study and education.

In considering the problem of conservation we must first deal with the vegetation, because it forms the natural covering of the country and is the ultimate basis, directly or indirectly, of all animal life. When we preserve vegetation we automatically preserve the greater part of the animals which inhabit it, since these are small invertebrates. The larger animals require separate consideration.

The land of Great Britain, especially the lowlands, has been subjected for so long to human occupation and cultivation that little indeed remains in a completely 'natural' state. Apart from the towns and villages, and isolated buildings, the railways, roads, aerodromes, and factory sites, the mines and quarries, most of the lowlands are occupied by farm lands under arable crops or fields of 'permanent'

* *Nature Conservation in Great Britain*: Report by the Nature Reserves Investigation Committee, March 1943.

grass. Scattered among these, however, there are woods, and here and there commons covered with heath and wild grasses, largely on soil which did not repay cultivation, at least in earlier times, and used by the 'commoners' for pasture and for the collection of dead wood. As a result of such uses they are often markedly altered from their original condition, though they still bear wild vegetation. On the uplands the picture is different. Cultivation may extend to the height of a thousand feet or more, but above this altitude most of the land is still occupied by natural plant communities. Except at the highest altitudes and in the most remote places the great bulk of the upland country has been used for pasture. Much of it, like many of the lowland commons, is covered with a vegetation of wild grasses and is known as 'hill' or 'rough grazings' largely used for sheep rearing in the great wool industry of past centuries. These include the downlands of the south, much of the uplands of the south-western peninsula, and of the hills and mountains of Wales and the north of England, the Scottish Southern Uplands, and the Highlands. Most of the grassland of these hill grazings owes its present condition largely to the continual nibbling of the sheep. Great tracts of land in the north, however, are not covered by pure grass vegetation, but by heather, bilberry and similar plants, often mixed with grasses, and these moorlands are frequently preserved as deer forest and grouse moor. Much of this land too is covered with bog, or boggy moorland, especially in the very wet climate of the north-west. Above 2000 ft., and especially above 3000 ft., the so-called 'alpine' vegetation begins to appear, and this is little if at all altered by human activity.

Thus the uplands of Great Britain are mainly covered by vegetation which is 'wild', in the sense that the plants composing it are native to the country and have come there by themselves, but nevertheless owes its particular character to human agency, mainly to the constant grazing of sheep and cattle. Vegetation of this kind is spoken of as 'semi-natural'. Much of the greater part of the land below 2000 ft. was originally covered by forest or scrub, and this woody vegetation has been removed by felling and clearing to provide fuel and timber for human use, to make room for sheep and cattle grazing, and in the lowlands for agriculture.

Though the lowlands and the lower slopes of the hills were once covered with forest, existing remains of native woodland are very scanty. Not much more than 5 % of the land area bore woodland of any sort in 1920, and this included modern plantations. Of the old native deciduous forest, consisting of oak, beech, ash, alder and birch, that which was not cleared was maintained for the supply of timber, small wood, and bark for tanning, though the native timber supply became so scanty several centuries ago that most of the demand had to be increasingly met by importation. Some of this native woodland still remains in a more or less natural condition, and woods dominated by all five of the trees mentioned are represented. Many of these woods have been planted up, mostly on the sites of old woodland, and have assumed most of the characters of natural woodland, though this does not apply to the modern conifer plantations, which introduce quite different conditions. The beechwoods of the southern chalk, the ashwoods of the Derbyshire dales, the oakwoods of the northern and western valley sides, the alderwoods of undrained marsh and fenland, the birchwoods, and the few remaining native pinewoods of the Scottish Highlands, are all genuine representatives of native woodland.

The still undrained marsh and fenlands which remain bear their own characteristic vegetation, but often determined in its detail and distribution by human activity. A very few 'raised bogs' of the kind characteristic of the central Irish plain still survive in the west and north of Britain, and they possess an extremely distinct plant population. The aquatic vegetation inhabiting rivers, lakes, pools and canals is again quite distinct and largely unmodified, though it may of course be destroyed, by man.

Finally, there is the vegetation of the sea coast, of the salt marshes, sand dunes, shingle beaches and sea cliffs. Because it is under the control of the constant and powerful influence of the sea this maritime vegetation, where it has not been destroyed and replaced by artificial constructions, is perhaps least modified by man of all the types, except the fresh-water vegetation and that of the high mountains.

The only way to safeguard and maintain such tracts of this remaining wild country as can and should be preserved is to set aside certain areas and control them more or less closely, according to their nature. Besides the tracts of wild and semi-wild country briefly described above there are a number of man-made habitats which support animals and plants of great interest to naturalists. Such are the hedgerows of the south and the low stone walls of the north, the embankments and cuttings of railways and roads, the exposed faces of disused quarries, and so on. Some of them, for example hedgerows, are threatened by ill-judged and hasty measures against pests, and though some destruction of these habitats may be necessary, careful consideration of all its implications is wanted before widespread action is taken.

Before we deal with the methods and details of control, it is necessary to consider the various objects of the efforts at preservation.

2. AIMS AND OBJECTS OF NATURE CONSERVATION

The first object of nature preservation on a large scale, and the aim which naturally and rightly meets with the most widespread interest and support, is the

maintenance for enjoyment by the people at large of the beauty and interest of characteristic British scenery. This depends at least as much upon the vegetation by which the landscape is covered as on its physical features. To preserve unspoiled and free from the chances of 'development', which wholly destroys its character and charm, as much as possible of this landscape is a duty we owe to our descendants, just as obligatory as the duty of securing conditions which will tend to their economic prosperity. As the National Parks Committee wrote in their *Report* (1931), this characteristic scenery is 'of peculiar interest to the nation as a whole—typical stretches of coastline, mountainous regions, moor and downs, river banks and fen. These areas constitute an important national asset, and the nation cannot afford to take any risk that they will be destroyed or subjected to disorderly development.' Under existing conditions destructive changes are possible at any time and place as a result of the activities of the speculative builder, of the establishment of new factories or other industrial or public works, of mining and quarrying, and also, though in a different way, of the activity of the Forestry Commission.

In the age of large private estates, which frequently included beautiful scenery, destructive development was often effectively prevented by the pride of owners in their possessions and their frequent refusal to part with or lease their land even when this would have been extremely profitable. Access to beautiful estates was often, however, refused in order to maintain privacy or in the interests of game preservation. Both maintenance of a beautiful estate intact and permission for access to it depended in any case on the interests or caprice of the landowner. Now that we are passing into a time when the wealth and power of large landowners will probably be increasingly and drastically curtailed, this precarious safeguard of rural beauty will disappear and public action becomes the only means by which it can be preserved.

It is fully realized of course that building and economic development must continue. We must house our people adequately, we must build new factories and construct public works, and we must maintain and improve our agriculture and increase our supplies of home-grown timber. But in addition we must see that we do not hand down to our successors a defaced and ugly land. In particular cases decisions between rival claims to the use of land may well be difficult. Compromise and give-and-take will be very necessary in the 'country planning' that will have to be undertaken, and not only between different possible economic uses but also between these and the preservation of natural beauty. It is true, of course, that much English rural beauty depends upon the villages and agriculture of the past, and how far it can be maintained with the changed agricultural methods of the present and future remains to be seen. But that is a separate question which does not immediately concern us here. Many British landscapes depend for their charm on the stretches of natural and semi-natural vegetation which still survive—the downs, the heaths and moors, many still unspoiled stretches of sea coast and certain tracts of well-wooded country.

Besides the paramount motive of the preservation of rural beauty there are others which are also of great importance. These may be described as the scientific and the educational, and it is the first of these and by implication the second with which we are mainly concerned in this Report.

Our native species of plants and animals, their distribution, habits and relationships, have long been a major interest of British naturalists, who have been increasingly disturbed by the progressive disappearance of species from many of their old habitats as the advance of urbanization destroyed the natural conditions. But it is the rise in importance of the modern study of ecology that has brought into prominence the seriousness of this threat to our native flora and fauna from the scientific as well as from the aesthetic point of view. Ecologists are not only interested in plant and animal species as such: their subject of study is largely the natural aggregations of species and individuals, or plant and animal 'communities' as they are called, that occur in nature. The preservation of sufficient unspoiled examples of these is an essential condition of their work. Plant and animal communities do not consist wholly or even mainly of specially striking or rare species whose diminution or disappearance is deplored. Plant communities are usually dominated by quite common plants, whose presence in great numbers is characteristic of particular conditions and at the same time helps to determine the presence of the host of other species associated with the dominants in the particular habitat. It is the community, the particular aggregation of species in a natural habitat, including those that are common, which is one of the most important objects of ecological study, and the preservation of sufficient examples of such communities is a primary ecological interest.

Oak, beech and ash trees, heather and bilberry and bog moss are very unlikely to disappear altogether from the country, but their continued existence as species is of very limited use to an ecologist if all the oakwoods, beechwoods and ashwoods, the heather and bilberry moors and the undrained *Sphagnum* bogs are destroyed or so modified that they no longer represent natural plant communities. Here the ecological interest almost exactly coincides with the aim of preserving the characteristic charm of British scenery so far as it depends upon natural vegetation. Our heritage of woodland, down and heath, mountain, moor and wild sea coast not only gives us relaxation and refreshment and the enjoyment of beauty but also indispensable objects of scientific

study. There is no conflict between these two interests—one may actually be made to serve the other. For appreciation of the natural beauty of landscape is greatly enhanced by the deeper understanding of it—of its geology, of the natural vegetation which covers it, and of the animals that inhabit it, as well as of the uses to which man has or may put it. And this brings us naturally to the third important object of nature preservation—that of education.

Nature study is now widespread if not universal in the lower forms and classes of our schools, and the modern teaching of geography is largely based on regional survey, which concentrates attention on the home region as a geographical unit that can be studied at first hand. In broad outline ecology is a natural development of both these subjects in all rural districts and in towns from which easy access can be had to the country. Knowledge of the nature and significance of our still unspoiled tracts of wild country should be taught alongside knowledge of the human uses to which the land has been or may be put. Only in this way can we educate our future citizens so that they may come to take a pride in the natural beauty as well as in the economic strength of Britain and to give their support to future developments that are wise and balanced.

The permanent success of the scheme for National Parks will depend on the use which is made of them and on the extent of the interest and enthusiasm that can be aroused. Public support to the necessary degree can only be created by greatly increased knowledge, understanding and appreciation of the natural interest and beauty inherent in scenery and vegetation. Both school and adult education on these lines is necessary, and ecological knowledge in the widest sense must be the basis of it. The formation of 'nature reserves' in which scientific work on natural and semi-natural plant communities and their accompanying animals can be carried on will not only advance an important branch of biological science which can be applied to the management and control of a considerable fraction of the natural resources of the country (for ecological knowledge and ecological methods are, and will be increasingly, used in forestry and certain branches of agriculture), but may also be made to contribute, in ways indicated later, to the success of National Parks through the development of public knowledge and appreciation.

Thus the various aims and objects of nature preservation, widely different as they appear to be, are in reality very closely linked. The values involved are first of all those which are now commonly, though most inadequately, described as 'amenity' values. These are perhaps the most important of all, since they touch the deepest sources of mental and spiritual refreshment, both conscious and unconscious, and of these the specifically aesthetic value is really a part. Then there are the scientific, the educational, and indirectly the economic values, and each, as we have seen, reinforces the others. The case for extensive, carefully and scientifically planned, nature preservation thus becomes extremely strong.

3. THE SOCIAL BACKGROUND OF NATURE CONSERVATION

The whole problem of nature conservation requires to be viewed against the human or social background.

The greatly increased pressure of the human population on the native flora and fauna is due not only to increase of population, but also to the much quicker and deeper penetration of modern means of transport. Comparatively remote places are now visited by many more people, who unwittingly, and often through mere numbers, tend to deface their beauty and destroy them as habitats for the native plants and animals. Increased mechanical and chemical means of destruction bear hardly on both plants and animals. The higher vertebrates suffer severely from shooting, trapping, netting, poisoning, and now gassing. This, of course, is intentional destruction, but active forces of destruction require active measures of conservation. Just what should be destroyed and what preserved must become a question of public policy. Ultimately a sound conservation policy must be based on an ecological expression of the resultants of different desires which are often in conflict.

In its general aspect the problem appears as that of resolving a fundamental conflict between conservation on the one hand and development in its widest sense on the other. Greater development of the country's natural resources is inevitable if Britain is to retain her position among the leading nations of the world: at the same time a national scheme of conservation becomes an urgent necessity if we are not to hand down to our descendants a land hopelessly impoverished in a most precious part of its heritage. This conflict is not merely one between rival interests. Conservation is not a sectional interest. Its importance to the community as a whole is comparable with that of development and is inextricably knitted up with efficient development. The ecologist who advocates it can do so in full consciousness of his membership of the whole community and as part of his special duty towards it.

There are many forms of development and their relations to the problem of conservation vary greatly. In the first place there is the building of new towns and villages or extensions to those already in existence; the erection of new factories, power plants, dams, locks, harbours, quays and so forth; the provision of new roads and railways, of new aerodromes and sports grounds. The relevant problems of planning and siting have been discussed in the Scott Report and your Committee would wish to support the recommendations there made for responsible and sympathetic control.

Of wider and more immediate significance to your Committee is the utilization of land for agriculture and forestry.

The land of Great Britain, so far as it is not used for housing the population and for industrial purposes in the widest sense, is mainly devoted to agriculture. Excluding the rough grazings of the hillside grasslands and moorlands, which bear 'wild' vegetation, about two-thirds of the area of England and Wales and about a quarter of Scotland was agricultural land in 1938 (*Agricultural Statistics*, 1938). Woodland of all kinds, on the other hand, only occupied a little more than one-twentieth of the land surface. The great increase of agriculture during the war has been mainly represented by the conversion of 'permanent grassland' to arable, though some areas of heath and hill grazings, as well as semi-wild fenland, have been ploughed. Most of this 'permanent grass' was former arable land that had been 'laid down to grass', i.e., sown with grass seed, or had been allowed to 'tumble down' to grass by pasturing derelict arable land which became colonized by grasses. All such land formed part of the agricultural system, and what has happened is a change in the balance of that system, so that for the most part the creation of new arable does not represent a destruction of wild vegetation. It is unlikely that the total arable area will be further increased to any extent because the limits of existing land that would repay cultivation have nearly been reached. We must, it is true, make an exception of the 'improvement' of hill pasture by ploughing, manuring, and sowing with clovers and improved strains of grasses, as advocated by Sir George Stapledon. This involves great changes in the composition of the herbage of existing rough grazings which have never been ploughed or manured, are composed of entirely wild vegetation, and cover a very great proportion of the hillsides of the north and west of Britain. The existing areas of hill pasture are so large, however, that a considerable number are likely to escape such treatment and should still be available for ecological work. Furthermore the 'improvement' of hill pasture scarcely alters the scenic character of the landscape. Yet the ecologist must keep in mind the extent of the changes brought about in this way and must secure the conservation of sufficient areas of the more natural hill vegetation for his adequate understanding of the problems which the new agriculture will raise, and of the results of the large-scale experiments which the new methods will constitute. Such understanding will form a large part of his claim to act as an expert adviser in agricultural planning.

The plans of the Forestry Commission for the afforestation of Britain are of very great importance to the ecologist. Our native woodlands are of special and unique interest to him because they represent the final and highest type of natural vegetation over much of the country. At present woodlands, including all plantations, only cover about 5·5 % of the total land area; and these, apart from a few tiny fragments, have been greatly modified by past treatment. The native woodlands are of deciduous trees, chiefly of oak, beech, ash, birch and alder, except in certain areas of the Highlands where the native Scots pine still persists. The replacement of this deciduous woodland by plantations of exotic conifers, or even of Scots pine in parts of the country where it is no longer native, involves a more profound alteration of a smaller remnant of native vegetation than does the activity of the improving agriculturist. The changes in the landscape brought about by such replanting and by the planting of former rough hill grazings with conifers are also much more conspicuous than those due to agricultural improvement. Finally the large-scale experiments undertaken by the forester are expensive and of long duration. While they are of great interest to the ecologist, providing him with much new material and many new problems, he cannot but feel deeply concerned about their careful planning, since errors or failures will be difficult to rectify.

For these reasons your Committee feel strongly that they have a special responsibility to express their views on the relations between afforestation and nature conservation in some detail. They are further encouraged by the fact that the Forestry Commission has recognized the special interests of ecologists in its activities, has promised to give sympathetic consideration to their requests for the conservation of certain areas of existing woodland and has invited co-operation in tackling the problems of afforesting difficult sites.

Given its primary task of producing the kind of timber needed by the nation it cannot be denied that the Commission is bound to plan the formulation of extensive plantations of exotic conifers. By far the chief commercial demand (about 94 %) is for coniferous timber; and the areas, poor or useless for arable agriculture, on which most of the new planting has been done, are chiefly areas on which conifers seem to thrive much better than do the native deciduous trees. But young coniferous plantations, straight-edged, their trees neat in form and precisely aligned, their floors bare of the familiar woodland herbs, undoubtedly introduce into the landscape an alien feature which offends eyes accustomed to the luxuriant irregular beauty of an old native wood. And the offence is deepened where a familiar open hillside has its contours blanketed under masses of dark and sombre foliage. The feeling readily arises that these plantations constitute a deadly threat, not only to the old beauty of the countryside into which they intrude, but also to its wild life, both animals and plants. Nor are these fears unfounded. The flora and fauna of coniferous woods are very different from those of our deciduous woods. Some of the characteristic species of coniferous woods are natives

of the country and might quickly reach new plantations on open ground. Others, not natives, might gradually establish themselves through the chances of migration and transport. Many of the native species formerly living in the area would certainly be ousted, though some would probably persist. The flora and fauna of old deciduous woods replanted with conifers would certainly be profoundly changed.

It is necessary however to consider a matter which touches deep emotions so strongly with the greatest possible objectivity. The programme outlined in the recent White Paper on 'A Post-War Forest Policy' envisages the planting of 3,000,000 acres of open ground, chiefly rough hill pasture, out of a total existing area of over 16,000,000 acres of rough grazings. This would result rather in the introduction of greater variety into our landscapes than a wholesale destruction of their beauty, even if, as is likely, the greater part of 2,000,000 acres of existing woodland are also replanted with conifers—provided always that a substantial amount of native deciduous woodland is maintained. The plantations will lose much of their repellent uniformity and ecological poverty as they grow older. An old plantation of stately, well-grown larch or Scots pine with a ground flora of bracken, bilberry or blue moorgrass has great beauty, though of a different kind from that of an oak or beechwood, and this should be true also of an old plantation of Douglas fir or Sitka spruce. The management of such plantations on silvicultural systems which do not involve clear felling, such as the 'selection-system', or, where the practical disadvantages of this are too great, one of the varieties of 'shelterwood', and which permit of self regeneration where viable seed is produced, is highly desirable both aesthetically and ecologically. It is still doubtful how far the productivity of pure coniferous woodland can be maintained in this country, at least on certain soils which show progressive deterioration as the result of the accumulation of coniferous humus, and it may turn out that mixed plantations of conifers and deciduous trees have a wide future in British forestry. The ecology of such mixed woods would be of great interest and thorough investigation of the soil problems involved is much needed.

The expert knowledge upon which such decisions should be based depends on real understanding of the ecological problems involved. This is the most vital consideration, not only for the ecologist but also for the forester himself and for the whole community. Comparison of a coniferous plantation or a mixed crop of coniferous and deciduous trees with a nearby natural wood of native trees is an indispensable step in the acquisition of such knowledge. The interests of the most ardent lover of our English and Scottish landscapes, of the most devoted naturalist, and of the most commercially minded forester, alike demand that there shall be conservation of as large an area as possible of our surviving native deciduous woodland. This should be well distributed over the country so as to include the widest possible variety of sites and of woodland types. Some might well be managed as exploited woods, others should be left quite untouched. In dealing with deciduous woods which are maintained as such it is most desirable, wherever possible, to secure self-regeneration, and this could probably be done in many cases by taking suitable measures, especially by excluding or reducing the numbers of animals which destroy seedling trees. An increase of predators, especially birds of prey, as suggested in Section 4 (v) of this Report, would keep down the destructive small rodents and would both protect the young trees, making regeneration easier, and establish a more varied and interesting wild animal life.

The Southern English climate, especially on the loam and clay soils, is essentially a climate of deciduous woodland, which is a characteristic feature of the landscape whose loss would be a major disaster. Much of it is now in a deplorable condition, partly owing to long neglect and partly to the intensive exploitation of war time. A great deal of this must be replanted, whether with deciduous trees or conifers, but some could be rescued and improved by appropriate measures.

The principal natural forest types, examples of which should be maintained, are the different varieties of beech and oakwood of the south, the durmast oakwoods on siliceous soils and the ashwoods on limestone soils of the west and north, and the remnants of oak, birch and pine wood in the Scottish Highlands. It is pleasing to be able to record that the Forestry Commission has already set aside two areas of old woodland, one in the High Meadow Woods by the banks of the Wye, the other in the New Forest. These will be left completely undisturbed as permanent forest reserves. Thus it is evident that the Commission is prepared to play a leading part not only in timber production but in nature conservation and the progress of ecological knowledge, and we should like to see the closest co-operation between all these interests.

Your Committee feel that the Forestry Commission ought to have a broader mandate now that its practical control of much the greater part of British woodland is being contemplated. There are many ways in which a largely increased forest area administered by a central authority would touch the life of the people as a whole. Among these are the relation of forests to water supply, to erosion by wind and water, to the provision of shelter for man, his crops and stock, to the conservation of wild life, and the general contribution of forests to scenic beauty and amenity. We should like to see the Commission concern itself actively with all these things, by close co-operation with other interested bodies and by the exercise of wider powers. The British people are not, at present, 'forest-minded', but they

might be increasingly made so by suitable educational propaganda, and there is no reason why they should not become proud of the national forests as an integral part of rural Britain. Such a broadening of the official outlook would awaken a sympathetic response in quarters at present lukewarm, or even hostile, to plantations seen only as crops of trees for the production of timber. In a word, if British forestry is to play a really worthy part in national reconstruction its aims should be much wider than the meeting of a national need for increased timber supply and the provision of a sound long-term 3% investment.

Your Committee would wish then to emphasize the common interests of the forester, the ecologist and the naturalist, to welcome their increasing collaboration and to urge that it should be carried further still. They appreciate the strength of the economic pressure which compels the Forestry Commission to plant conifers more extensively than our native deciduous trees. They ask, however, that silvicultural systems other than clear felling should be practised as widely as possible, and that areas entirely composed of native trees should be planted wherever it is economically reasonable to do so. Finally they recommend very strongly the conservation of considerable areas of existing natural woodland as indispensable material for highly relevant scientific investigation, as well as for the other more immediately obvious reasons to which reference has been made.

Another important field of conflict is seen in the activities incidental to game preservation. Game preservation, it has been truly said, is the only form of wild life management with any history or tradition in Britain. Its object is to protect certain selected animals (almost all of which are birds), so that later on they may be killed for sport. They must be provided with suitable habitats and their enemies must be destroyed. This line of action has had two opposite effects on wild life. Preserving the suitable habitats of game often means preserving considerable tracts of natural or semi-natural vegetation with the animals that inhabit them, so far as these are not hostile to the game itself. On the other hand, the carnivorous birds and animals which prey upon game are ruthlessly destroyed, resulting in a very great decrease in the populations of predatorial species. This in its turn has led to a great increase of small rodents—mice and voles, rats and rabbits—which are a principal food of the predators—with resulting serious and widespread damage to agricultural crops and seedling trees. One conspicuous predator—the fox—is protected, though not without some friction between the hunting and the shooting interests, where these are separate. The status of several of the animals involved is considered in Section 4 (v). Another effect of game preservation on a large scale is the high local density of certain species of game, including ground game, which press hardly on agriculture and silviculture. Not only the pheasants and rabbits of the lowlands, but the large populations of red deer in the highlands do much damage to crops, and the latter to trees. Again excessive density may result in serious epidemic disease, e.g. grouse disease.

It is, however, only just to recognize the important effects of game preservation in the maintenance of natural habitats, not only extensive heaths and moors for grouse and deer in the west and north, but also the deciduous woods and copses used as pheasant preserves and fox coverts which are the habitats of many of our wild flowers and small birds. If game preservation were to cease entirely and no other form of protection put in its place, the whole countryside being devoted solely to the economic interests of agriculture and silviculture, we should lose at once the great majority of our still-existing wild life habitats.

It would seem that the shooting and hunting interests should submit to a certain curtailment of the privileges they have enjoyed in the past, but it is difficult to envisage a Britain in which this kind of sport was wholly suppressed. If sportsmen would tolerate an increase of predators, would raise fewer pheasants, and be content with a lower density of foxes and red deer in those regions where they are now excessively abundant, considerable progress could be made towards a juster balance of nature.

Love of the countryside, including its wider aspects, has certainly not decreased in the population at large during the present century. Indeed, it has been fostered by the freer range of townsfolk through the country made possible by motor transport. Besides the thoughtless people who tend to deface it there are many who earnestly desire to see its natural beauty and interest preserved. Among the more special interests the love of wild birds has increased enormously, as is shown by the work of the Royal Society for the Protection of Birds, which has been active in securing legislation. A recent writer has remarked that the British birds are 'perhaps the most written of...listened to, protected, loved birds in the world'. Their few 'tens of millions have a public not many times smaller in numbers than themselves'. This widespread and intense sentiment can no more be ignored than the Englishman's love of sport, and both must be balanced against purely economic interests. No greater mistake can be made than to minimize the importance of sentiment, to seek to brush it aside as rather a shameful weakness. Sentiment, like other human qualities, can be unduly exalted and misused, but it remains one of the most important and inescapable of human motives, and must be given its just place in social organization.

All such factors as those which have been discussed must be taken into consideration and given their due weight before a sound conservation policy, or any comprehensive planning of land utilization can be devised. The claims of agriculture should come first—that is common ground—but by far the greatest advance here is to be made by improving the cultivation and management of land already used as arable or pasture rather than by bringing extensive new areas into the agricultural regime. The claims of forestry in the proper management of existing woodland and the establishment of extensive new forest areas may perhaps be regarded as coming only second to those of agriculture in national importance. They can be met with all reasonable regard to nature conservation, sport and public amenity if only wide vision and careful broad-scale planning are adopted. This is all-important in the development or conservation of such land as still remains in a wild or semi-wild state. Ecological knowledge, already existing, or accessible to properly directed research, is the essential foundation of any scientific handling of the problems involved. Both the social, the economic, and the ecological facts are indispensable data, and none can be neglected if successful solutions are to be found.

4. METHODS OF NATURE CONSERVATION

(i) *Vegetation*

The indispensable general method of preserving wild plant life together with the small animals which accompany it is to set aside certain areas in which destruction and disturbance can be prevented. This method is not however adequate for the larger birds and mammals, which have to be considered separately (see Subsection (v)).

It has long been proposed to establish a number of *National Parks*, rights in which would be acquired by the State primarily for the enjoyment of the public, in parts of the country famous for the beauty of their scenery, and this proposal will almost certainly be carried out. Such parks will automatically preserve considerable areas of wild vegetation. But National Parks alone will by no means cover the whole of the requirements. In the first place there will be too few of them, and secondly they cannot be managed with primary regard to scientific needs. These require the maintenance of many areas quite unsuitable for the formation of a National Park and very widely scattered through the country.

In addition to the National Parks it is proposed in the N.R.I.C. Report (pars. 15, 16) that a number of large *Scheduled Areas* should be established, and that in these 'development' should be restricted, so that within such areas the main features of natural beauty would not be destroyed, and much natural vegetation would be preserved.

But for purposes of scientific work it is necessary to preserve a considerable number of areas which are generally much smaller, chosen because they represent natural habitats bearing single or several plant communities, and these may be specifically called *Nature Reserves*. Some of the Nature Reserves would naturally fall within the boundaries of the National Parks and Scheduled Areas, but others would lie outside them, and all would require a different type of management from the National Parks.

It has been proposed by the N.R.I.C. that Nature Reserves should be divided into two categories—*National Nature Reserves* and *Local Nature Reserves*. The former, it is suggested, should be acquired by the State, supported from national funds, and administered under a State Authority. Together they should represent all the important British types of natural habitat and natural plant community. Local Reserves, on the other hand, would be acquired or held locally under various arrangements with their present owners, and local, including local educational, authorities would be represented on their governing bodies. The Local Reserves would supplement the necessarily restricted number of National Reserves and could be used for a variety of purposes, scientific, educational and 'amenity', according to their nature and the conditions of their tenure.

In considering the actual administration of Nature Reserves it is essential to recognize, first of all, that informed and careful management is in fact necessary for nearly all reserves as well as for National Parks. A great deal of the vegetation which it is desired to preserve is partly the result of human activity through the centuries. In other words it is 'semi-natural' and not wholly 'natural' in the sense of being the product of 'Nature' alone. This is true for example of downland, of the hillside grasslands and many of the moors of the north and west, of much heathland, of undrained or partially drained fenland, and of most of our deciduous woodland, whether the trees have been planted or not. These types of country together make up by far the greater portion of the regions of which relatively large samples should be preserved. In order to maintain any area of this semi-natural vegetation more or less in its present condition the existing human activities (grazing, burning, mowing, coppicing or selective felling) must generally be continued. This applies to the strictest nature reserve or sanctuary as much as it does to any area to be established as a National Park. If the human activities cease the vegetation immediately begins to change. The formerly grazed downland, the periodically burned heath, the fen which was regularly mown, becomes colonized by shrubs and often by trees. When the human activities cease, the character of the area is wholly altered,

and the plant communities with their characteristic animals, which it was desired to preserve, disappear. If coppicing is discontinued in a wood of the 'coppice-with-standards' type, the shrubs become 'overgrown' and the ground vegetation is seriously impoverished owing to the dense shade created. Thus if you 'let Nature alone' in such areas you frustrate the very aim you have in view. With the changes in the plant communities which she immediately initiates the conditions of life are altered and the interesting or rare species which depended for their existence on the former (man-made) environment may disappear altogether.

Areas in which human activity was abandoned some time before reservation show all stages of these changes, the nature and exact course of which are vital subjects of ecological study. For this reason such areas should in general be left to develop their own natural vegetation, and the same is true of certain parts of all newly reserved areas, which should remain undisturbed while most of the reserve is kept in the 'semi-natural' condition that was produced and maintained by human agency. Thus, most of the old-established fen reserve at Wicken in Cambridgeshire is kept as 'sedge fen' or 'litter fen' by clearing invading bushes and periodical mowing, which are essential to preserve for naturalists the fen plants and animals, while small portions are allowed to grow up to the scrubwood community called 'carr'. The same procedure, *mutatis mutandis*, should be adopted in downland or heath regions, where grazing or burning should be continued, except in certain selected portions in which shrub and tree colonization should be allowed. Where it is impossible or undesirable to continue the previous regime, some alternative procedure having a similar effect must be adopted. For example, colonization of heathland by trees, which has been constantly checked or prevented by periodic fires, may also be stopped by uprooting the tree seedlings or saplings.

Areas which have always been free or almost free from human interference are relatively few, but naturally of great ecological importance. They include parts of the sea coast where new soils are accumulating, a considerable number of ponds, lakes and rivers and their margins, and high mountainous regions. In such places we see new plant communities in process of development, and their continued freedom from interference is of first importance to ecologists. They are also of high value because they represent the fragments of really 'wild' nature still existing within the country. Reserves of this nature require much less 'management' than the 'semi-natural' areas which owe their character partly to the continued activity of man.

It will be clear from what has been said that for the great majority of reserves expert management is essential if they are to fulfil their purpose, and this is true alike of National Parks and of both National and Local Nature Reserves. Any nation-wide scheme of reservation must provide for such administration, and it is ecological knowledge combined with practical experience of land management which is necessary.

If a series of National Parks is established by the State, a primary aim must be to preserve the beauty of the scenery they include. This cannot be done unless the natural vegetation is substantially maintained, for the beauty of most scenery depends at least as much on vegetation as on the physical features which it covers. A great deal of the ecological knowledge required has been gained during the past quarter century, and this is being steadily increased as new studies are undertaken. Here we have the natural source not only of the technical management of Nature Reserves, but also of the technical advice needed for preserving the character of National Parks. It is proposed by the N.R.I.C. that there should be separate authorities for National Parks and National Nature Reserves, and this would probably be a sound arrangement because the problems involved in the administration of the two are in several respects different, but the function of ecologists in advising on those problems which depend on the maintenance of natural vegetation in the parks cannot be ignored. Further work on the protected reserves will continually throw fresh light on such problems and increase the weight of the advice that can be given on the treatment of areas of similar nature within the National Parks.

(ii) *Invertebrate communities*

It is not generally realized what an enormous proportion of the total fauna, both in numbers of species and in numbers of individuals, is contributed by the invertebrate groups, nor how few of these, outside those groups (such as butterflies, moths, beetles and snails) which attract the collector, are known to, or are even seen by, the average naturalist. Nevertheless, after plants, they constitute the most important element in the preservation of any population in its natural balance; nor in many cases could the plants themselves subsist without the ubiquitous activities of these animals. The extreme complexity of their specific interrelations, their vital effects upon the soil, their attacks upon the plant elements, from the minute fungi and algae to the largest trees, both as direct feeders and disease carriers, and their essential place in the food chain in providing food and as predators themselves, set problems of the highest scientific and economic importance. Fortunately, the great majority of these communities and species are automatically protected by the preservation of the type of vegetation in which they find their natural habitat, and little more need be done beyond maintaining the existing plant balance and securing that the breeding stocks of the few more showy rare

species are not reduced below the danger point by the depredations of collectors.

Because of these facts and their economic implications it is a prime need to secure the preservation of a sufficiently representative series of invertebrate communities so that their intricate relations can be closely studied in the balanced state which they have achieved under particular representative conditions. The preservation of areas which include representative plant communities will, to a large extent, achieve this object; but there will be other areas—particularly perhaps among semi-natural and man-made habitats—where preservation should be based upon the existence of important invertebrate populations and species.

(iii) *Fish*

Angling is so widespread a sport, appealing to such large numbers of the public, that the conservation of fish has behind it a really powerful interest. Practically all fresh waters are regularly fished, and the anglers, often through their clubs and associations, backed by the fishery boards, are probably strong enough to see that fresh-water fish populations are not seriously reduced.

The pollution of rivers and streams, both by industrial effluents and by sewage, is by far the greatest factor inimical to fish. A good deal has already been done to reduce this evil, but more general and stringent measures should be taken. Conservation of particular lakes, rivers and streams is probably unnecessary for the preservation of fish, as such, though there are many ponds and small lakes which ought to be reserved, with surrounding land, in order to preserve the plant life and accompanying animals—water birds and others. Such action will, however, often reduce the free water available for fish and thus work against the angling interest: it may in fact ruin the water from the point of view of the fisherman. This conflict can be resolved in some cases by appropriate management, providing for periodical partial clearing of vegetation, in other cases by abandoning the attempt to preserve the fishing as well as the vegetation and the other animals. Taking a wide view, the relinquishment of angling in a limited number of fresh waters will not seriously restrict the opportunities of fishermen.

There are, it is true, a few very local species of fish, such as char and species of *Coregonus* in some lakes, but these are not, on the whole, much sought after by anglers, and there is no serious danger of their numbers being reduced.

The adoption of more effective means of preventing the pollution of fresh waters, such as the setting up of Regional Boards, based on catchment areas and responsible for all matters pertaining to the purification of sewage, industrial effluents and polluting storm waters, as recommended by the Pure Rivers Society, is by far the most important measure that can be taken for the conservation of fish and the other aquatic animals and plants essential to their existence.

(iv) *Amphibia and reptiles*

Most of the twelve native species belonging to these two groups are of widespread distribution in the country and in no particular danger, but a few are local and need protection. Of these the natterjack toad is confined to sandy areas, both coastal dunes and inland. Its occurrence on certain dunes, such as those of the Lancashire coast, furnishes part of the case for reserving such areas. The edible frog is not a native, but has been introduced to certain places in the past and may still survive in some areas. If so, it might well be preserved as an interesting form which is not known to be seriously inimical to native species.

The smooth snake is a very interesting species apparently confined to the New Forest and sandy areas in neighbouring counties. It is a harmless snake feeding chiefly on sand lizards, slow-worms and small mammals. The sand lizard is another interesting species with a discontinuous restricted range, occurring both in the same region as the smooth snake and also on the Lancashire dunes.

The distribution of these two reptiles and the natterjack toad therefore form one good reason among many others for forming reserves (probably National Reserves) in both these regions.

(v) *Birds and mammals*

Different considerations apply to conservation of the higher vertebrates, the warm-blooded birds and mammals, partly because of their great powers of movement and partly because certain kinds directly involve human interests. These animals cannot be conserved simply by a passive policy of setting apart particular land areas as reserves, though this is necessary to protect certain breeding stocks.

The problem always eventually becomes one of attaining and preserving a certain density and distribution of the population of the species concerned in different parts of the country. This involves positive and active management which cannot be planned and carried out without knowledge gained by research and application of the results of research to the field problem. It is useless to attempt to preserve a sample of the animal population as one preserves a library, museum or ancient monument. Carefully calculated methods of conservation and control are even more necessary here than in the management of reserved tracts of wild vegetation.

Even in the United States with its huge wild life parks the passive policy of simply making such reserves, however large, has often conspicuously failed adequately to protect wide-ranging species such as migratory birds; and elk (wapiti) have been systematically shot by 'sportsmen' at their points of passage into and out of the parks.

(*a*) *Complexity of the factors at work*

Besides the special research and active management required to control each species the proper balancing of various material and cultural claims is necessary as a preliminary to a decision as to the precise aims of control. Adequate publicity and the promotion of public knowledge and interest by education are also required to obtain a secure foundation in popular support for the measures taken, just as they are for the proper support and use of National Parks.

The sectional interests involved give rise, as we have seen, to very different human attitudes towards different kinds of animals. Perhaps the most conspicuous instance, already discussed in general terms, is the attitude of shooting men to different species according to whether they are suitable objects of sport or whether, on the other hand, they prey on those objects. Thus shooting men wish to increase the populations of the native black game, woodcock, red grouse, common partridge, and the introduced French partridge and pheasant, while they want to see diminished or wiped out the native populations of sparrowhawk, magpie, carrion crow, stoat, weasel, red fox, polecat, hedgehog, as well as the introduced little owl, grey squirrel, brown rat and domestic cat—or at least the 'hunting cats' of the countryside. Since there are shooting rights over probably 80% of our farmland, excluding the large areas of hill grassland, the dominance of the shooting interest has led to a great scarcity of predators following upon the perfection of modern small arms and efficient 'game-keeping'. The fox is an exception because much as the shooting man dislikes the animal the hunting man insists on its preservation. Some sort of compromise has been arrived at between the two interests—the less difficult because the same people often pursue both sports.

The rabbit was introduced to this country a very long time ago, and the variations of its status in public estimation through the centuries and at the present day, afford an excellent example of the conflict of interests. At first rabbits were apparently scarce and fetched relatively high prices, but by the fifteenth century they may well have been as abundant as they are now judging by the numbers provided at certain feasts, and in the sixteenth century Gesner describes the 'copia ingens cuniculorum' in England. In the seventeenth century rabbits were highly valued as a source of food and fur, and so they have remained until quite recent years. In Scotland they were little known until the nineteenth century, when they rapidly increased so that they are now almost as abundant and ubiquitous as in England, except at high altitudes. They occur in great numbers on almost every island and islet round the Scottish coast, apparently always introduced by man, according to available records. At the present day the rabbit is valued by the sporting farmer, by the large landowner who preserves them in 'warrens' for rough shooting, by the fox-hunt which sometimes 'farms' them as food for foxes, by the professional trapper, by the hatmaker, by the poulterer and his customers, and by the poaching villager who likes to be able to trap or shoot an occasional rabbit to supplement his meagre larder. Most naturalists would be sorry to see rabbits disappear completely, and many members of the public find them very attractive animals. The progressive forester, farmer and market gardener, on the other hand, naturally regard rabbits simply as pests, and indeed in their pre-war numbers they did very serious damage to crops in certain districts, besides completely ruining great tracts of rough grazings. The overwhelming motive of conserving all foodstuffs in wartime has swept away opposition, and rabbit 'control', which in this case means wholesale extermination, has been established over large parts of the country. Nevertheless, there is a case for allowing the continued existence of a moderate rabbit population in some areas.

The war upon predators has resulted in a great increase in the number of small rodents—the mice and voles—and these do a great deal of damage to young plantations, besides having had a decisive effect in preventing the natural regeneration of our deciduous woods by eating off the seedling trees. The common vole multiplies excessively in young forest plantations which are often grown on hillsides open to walkers and naturalists as 'National Forest Parks' established by the Forestry Commission. In high density the voles damage young trees very severely, but in low density damage is rare. The presence of voles modifies the dominant grass vegetation and allows a number of flowers to become conspicuous, thus providing a more varied and attractive vegetation. The voles also bring to the hills an impressive fauna of predators such as buzzard, kestrel, long-eared and short-eared owls, which cannot live comfortably in areas where game is intensively preserved. By checking the growth of the strong coarse grasses, such as purple moor-grass (*Molinia*), which is often dominant on the damp western and northern hillsides, and by their constant burrowing, which aerates the soil, a moderate population of voles would probably actually benefit the growth of the young trees. Thus there is a strong case for maintaining such a population at a moderately low density.

Many more instances could be given of the complex tangle of motives, feelings, interests, habits and activities which affect the density and distribution of our higher vertebrate fauna, but two or three will suffice. The red squirrel is very widely regarded as a charming animal whose disappearance would be deeply regretted, but it certainly does shattering damage to conifers by ring-barking in the crown. The American grey squirrel, introduced on a ducal estate because of its attractiveness, has spread over wide areas and is certainly a more serious pest in plantations, especially of maturing conifers, than the

red squirrel, for whose widespread decrease it is probably largely responsible. On more than one Hebridean island visiting biologists have collected so many individuals of endemic races of mice as to endanger their existence, though they are of the highest interest to naturalists. Cornish fishermen would like the seals exterminated, believing that they endanger the supply of fish. Scientific surveys suggest that this is a mistaken view, though complete proof has not yet been obtained. The presence of seals adds a strikingly attractive feature to our coastal scenery.

In the post-war planning of agriculture, a wide range of policies has been advocated and amongst these it is proposed that hedgerows and small copses should be largely eliminated. Hedgerows, it is held, compete with the adjoining crop, may harbour injurious pests and weeds, and at the same time hold up the intensive mechanization of farming which is most effectively carried out in large fields. Such a policy if applied to extensive areas would largely destroy the beauty of much of the English lowlands. It would destroy the main habitats of many of our most cherished wild flowers and also the breeding places of most of our small birds. Moreover, though the breeding of injurious insects might be reduced by the abolition of hedgerows, in the opinion of many ornithologists the consequent drastic diminution of small birds would remove one of the most important checks on the insect pests of farm and fruit crops. Finally hedgerows provide shelter for farm stock and are essential as wind breaks for many crops. The removal of hedgerows and the filling in of the associated ditches may bring about on the lighter soils erosion both by wind and water. This is an example of the complexity of the problems and interests concerned when a policy seeks to change on a large scale the biological and agricultural balance of the countryside.

(*b*) *Introduced species*

At various times different landowners have introduced to their estates, for the sake of amenity or sport, a great variety of exotic animals, including Siberian roedeer, Japanese deer, Chinese waterdeer, wallaby, fat dormouse, and grey squirrel; among birds, little owl, Canada goose, bobwhite quail; among Amphibia and reptiles, edible frogs and Mediterranean green lizards; among fish, rainbow trout, sunfish and black bass. Fur farmers have introduced silver and arctic fox, muskrat, nutria, and mink. The three last named have escaped and spread, muskrat with seriously destructive results, though it has now been exterminated. The interest of some people in the new and the bizarre is often stronger than in familiar native species, and the introducers probably gave no thought to the effects of the strangers on our native animals, or on other interests than their own, effects which are sometimes very serious. It is suggested that the introduction of exotic species should be forbidden except under special licence.

(*c*) *Use of reserves for animals*

The use of a reserve for any particular species of animal is closely dependent on the size and movement of the animal in question and on the vulnerability of its breeding population. In Britain the main use of special reserves for vertebrates would be to protect (*a*) breeding stock, at vulnerable periods of aggregation (herons in 'heronries', gannet, shearwater, grey seal, etc.), (*b*) roosting aggregations of bats, and (*c*) very local species such as bearded tit, crested tit and bittern, including endemic island races of small mammals. Such reserves would form convenient places for long-term scientific work. On the other hand, many birds and the larger mammals are constantly passing from one area where they may be protected to another where they may be destroyed. Accurate knowledge of the habits of each species, which can only be obtained by research, is essential before effective measures of control* can be devised. The mere establishment of a reserve in which alone an animal is safeguarded is not sufficient.

(vi) '*Sanctuaries*' *or* '*Species Reserves*'

The word 'sanctuary' is often applied to areas reserved in order to protect rare or specially interesting species of animals or plants which are in danger of becoming rare. This is a highly desirable object, and it should be possible to protect a large proportion of such species by choosing for reservation at least some of the areas in which they naturally occur. Certain rare mammals and birds can only be effectively protected by safeguarding their breeding places and forbidding their destruction over considerable areas of wild country such as might be chosen as National Parks or Scheduled Areas, or over the country as a whole. Rare plants and rare invertebrates are much more narrowly localized and could often be safely included in comparatively small reserves.

The term 'sanctuary' was deliberately avoided by the N.R.I.C. in their report because its use sometimes implies a disastrous policy of 'letting nature alone'. Enclosing a reserve containing rare species while neglecting to maintain the conditions which enabled those species to exist and flourish results in changes which often lead to their disappearance. The processes referred to on p. 9 have free scope and the 'sanctuary' becomes a wilderness of the hardiest and most aggressive plants and animals. It may even become a mere 'focus of weeds and vermin' in the vigorous words of one critic. For this reason the N.R.I.C. use the term 'species reserve' instead of 'sanctuary'.

* The word 'control' is here used in its proper sense of 'regulation', not as synonymous with destruction, a sense in which it is now often misused.

The desire to save rare species from complete extinction, in order to prevent the permanent impoverishment of our fauna and flora which their disappearance would mean, is very widespread. It is felt by naturalists who are not ecologists, by ecologists themselves, and by many 'lay' members of the public. A distinct 'kind' of animal or plant is a natural focus of interest. It must always be so, since species are the fundamental units of our flora and fauna, and it is of aggregations of the individuals of particular species that plant and animal communities are made. Furthermore, the fact that a particular rare species is a natural member of a particular community is always of ecological interest, and the ecology, i.e. the conditions of existence, of a rare species may be of great significance. Hence the ecologist would always like to see rare species protected in the ways suggested, though rare species, as such, are not his *primary* interest, which is the study of species, whether rare or common, and of the communities which they form, in their natural habitats. For this reason ecologists could not possibly be content with limiting reserves to 'sanctuaries' for the preservation of rare species. To be effective a 'sanctuary' or 'species reserve' must be a sample of the particular community in which the rare species finds a natural home, and to preserve that species the community in which it lives, its proper habitat, must be preserved. The stress is therefore to be laid on preserving the community: if the samples preserved contain rare species their interest is increased, but the choice of reserves cannot be limited on that ground.

Some ecologists hold that it is of little use to try to preserve species which have been so persecuted that the breeding population has been reduced below the critical limit and recovery is unlikely. The kite, of which a few pairs only are said to remain in Wales, is given as an instance. The decline of a species owing to persecution must, it is argued, be arrested at an earlier stage if efforts to preserve it are to be effective. It is probable, however, that the strong sentimental urge to try to prevent a species which has become rare from disappearing altogether will always lead to an attempt to preserve the last remnants of its breeding stock in the hope that it may recover. It is important to remember that it is protection of the breeding stock and its habitat which matters. It is of little use to forbid the destruction of stray individuals.

5. MACHINERY OF NATURE CONSERVATION

We have now considered the main problems involved in nature conservation and the kinds of method necessary for their successful solution. It remains to deal with the machinery that must be set up if those methods are to be applied with effect, and we must first consider the methods of establishing nature reserves.

Hitherto such reserves as exist have for the most part been given by their owners or bought by public subscription and vested in bodies like the National Trust or the Society for the Promotion of Nature Reserves. A certain number belong to local bodies or trusts of various kinds, and some remain in the possession of private owners who have expressed the intention of keeping them as reserves, with the further intention, in certain instances, that they should ultimately pass into the hands of some body which would maintain them in perpetuity. It is clear that if any considerable part of our remaining wild life is to be conserved these haphazard methods are not enough, valuable as they have been in the past, and that some comprehensive and systematic plan must be adopted. In regard to conservation by the establishment of reserves the Nature Reserves Investigation Committee has taken the first important step by proposing a primary distinction, already referred to, between National and Local Nature Reserves.

(i) *National Nature Reserves*

'The...purpose...of ensuring the survival and semi-natural communities of plants and animals to provide material for serious studies can be met only by means of reserves in districts suitable to the particular wild life to be preserved; and the reserve must be managed in these interests and not with any other object. Their distribution bears no relation to arbitrary boundaries or centres of population, and their selection and conservation must be based on a single plan for Great Britain as a whole. Their management must be subjected to a unified direction with full responsibility at the centre...if their characteristic features are to be preserved, a continuing expert control must be established. Reserves of this kind are a national concern and will for convenience be referred to as National Reserves.'*

The kind of Reserve made for the purposes described in the passage quoted is called elsewhere in the N.R.I.C. Report a 'Habitat Reserve', and it is, in effect, a community or ecological reserve. The purposes described are those with which your Committee is primarily concerned. The proposal to establish a series of National Habitat Reserves under 'continuing expert control' and 'subjected to a unified direction with full responsibility at the centre', is one which has the complete agreement and support of your Committee.

The National Nature Reserves should include relatively large areas and embrace the set of successional plant communities characteristic of a particular type of natural habitat, e.g. down pasture,

* *Report of N.R.I.C.*, 'Nature Conservation in Great Britain', par. 7.

chalk scrub and yewwood, and beechwood, on the chalk downs. In some cases it would be possible and very desirable to include within one reserve two or more commonly adjacent types of habitat, e.g. saltmarsh, sand dune and shingle beach.

Large habitat reserves would serve as excellent sites for long-term ecological research both on plants and animals.

(ii) *'Habitat Reserves' and 'Species Reserves'*

Besides the Habitat Reserves the N.R.I.C. would distinguish 'Species', 'Amenity' and 'Educational' Reserves. The Species Reserves are intended to secure the survival of rare or very local species. Some of these would also come under central control as National Reserves. The term 'Species Reserve' was adopted by the N.R.I.C. in place of 'Sanctuary', as has been already explained, because of the unfortunate implications which the latter term sometimes carries. But the N.R.I.C. realize that there is no real scientific distinction between Habitat and Species Reserves since they state that 'Species Reserves must in fact be a special kind of Habitat Reserve, in that a species cannot be preserved in natural conditions apart from the communities within which it is able to thrive' (N.R.I.C. Report, par. 18 (ii)). Since this is undoubtedly true, it would seem that if a certain number of Habitat or Community Reserves were selected because they not only represent good examples of plant and animal communities but also because they contain rare or local species, as would be desired by all naturalists, that would meet the case. The regime of management would not differ, since it is the community containing the rare species which has to be maintained. We regard the statement that 'Species Reserves will usually be of smaller size than Habitat Reserves' (par. 18 (ii)) as rather dangerous. For example, supposing a rare species is confined, say to 2 acres within a particular more extensive habitat or community, it would be a mistake to confine the reservation to that area alone, even with a marginal safety zone. Narrowly localized species sometimes spread from their original area, and they may abandon it altogether and move to a neighbouring one: if only the area actually inhabited by the species at a particular time were reserved there would be no opportunity for such a move. It is always the type of habitat containing the species that it is important to safeguard.

(iii) *'Amenity' and 'Educational' Reserves*

It is not contemplated by the N.R.I.C. that Amenity and Educational Reserves should be National Reserves, since these 'subserve local rather than national needs' (par. 21 (ii)). Presumably 'national amenities' are considered to be sufficiently supplied by the National Parks, 'National Forest Parks', and 'Scheduled Areas' (see p. 16 of this Report). The N.R.I.C. Report (par. 15) calls attention, however, to the fact that many Scheduled Areas 'could be made to fulfil within themselves and by the simplest means all the three purposes of nature conservation', i.e. scientific studies, enjoyment of nature, and education in natural history. We regard it as important to stress the point that most, though not quite all, Nature Reserves, whether national or local, can likewise fulfil all these functions, and that it is most desirable that they should be made to do so. In this way they will be of the greatest use to the widest range of interests and will therefore obtain the largest measure of public support. There is no reason whatever why the public should not be allowed free access to a self-regenerating beechwood for instance, or any other type of natural or semi-natural wood, provided that they can be successfully deterred from damaging it, and there is every reason why it should be used for teaching students, both children and adults, some elementary lessons in natural history. Such woods are of primary interest and value to the ecologist as examples of important native types of vegetation with their naturally accompanying animals: many of them are of great and characteristic beauty, and they can all be used to notable advantage in education. The same may be said of many other types of habitat in which reserves should be established, such as downland and heath, sand dune, moor and mountain. It is only in a few cases, where the vegetation is easily destroyed or damaged by trampling, or rare species of birds or plants have to be protected, or scientific experiments are in progress, that public access would have to be restricted and regulated.

The conclusion seems to be that *all* Nature Reserves are really 'habitat reserves', that the maintenance of their value, scientific, aesthetic or educational, depends essentially on their proper management and that this must be ecologically instructed. The detailed regulations governing access and use must vary considerably according to the nature of the particular reserve, and only a competent management can properly decide what can be permitted and what should be forbidden in each.

(iv) *Local Nature Reserves*

'These would comprise areas the preservation of which is of local rather than of national importance.' 'They would be owned and managed by societies, local authorities or individuals' (N.R.I.C. Report, par. 21 (ii)). Habitat, Species, Amenity, and Educational Reserves are all contemplated in the N.R.I.C. Report under the category of Local Reserves. There are of course a considerable number of such reserves now in existence, and they serve very various purposes. Many belong to the National Trust, and most if not all of these have been vested in the Trust with the object of securing to the public the use and enjoyment of areas of natural beauty. They would fall under the N.R.I.C. class of 'Amenity Reserves'.

Some of them, however, such as Wicken Fen in Cambridgeshire, are in fact of greater scientific than 'amenity' value; others, such as Scolt Head and Blakeney Point on the north coast of Norfolk, are of great value from both points of view; and all of them, so far as they include natural and semi-natural vegetation, have some ecological value. The objects of the National Trust do not include nature conservation for scientific purposes, though in fact the existence and activity of the Trust have been instrumental in preserving areas which can be and some of which are actually used for such purposes. This is possible because the Trust properties are administered by local committees, and on some of these the 'natural history' interest is strongly represented, so that permission is freely given to qualified people to carry on scientific work within the Trust area. Though the Trust could hardly be so reconstituted as to fulfil the scientific functions of the authority responsible for *National* Nature Reserves, it would be of advantage to the formation of *Local* Reserves if it could add to its objects of preserving places 'of historic interest and natural beauty' by including 'scientific interest'. On important archaeological sites the scientific and the historical (or prehistorical) interests merge.

The Society for the Promotion of Nature Reserves has, on the other hand, the primary object of preserving areas of natural history interest and holds a few reserves acquired on this ground. These also are administered by local committees and in some of them ecological work has been carried out.

Both the National Trust and the Society for the Promotion of Nature Reserves are organizations of national scope, but many, probably the majority, of their properties, on account of their nature or of their geographical position, are mainly of local use, though visitors from a distance may not be infrequent. The N.R.I.C. would probably wish to class the bulk of these properties as Local Reserves. There are also other local reserves scattered through the country, intended for one, or more than one, of the purposes described, and with the ownership vested in local authorities, local societies, trustees, or private individuals.

Local reservation of areas for all the purposes discussed will undoubtedly continue to be made whether a national scheme of reservation is adopted or not, and since the reservations will usually be due largely to local effort the ownership and administration of such reserves must naturally be determined by local wishes. As in the case of National Reserves it seems unnecessary to divide such reserves into rigid categories, since they can so often be well employed for more than one purpose, and where possible it is highly desirable that the different functions should be carried on side by side. In this way and under enlightened management, the various interests can be harmonized, and a wider understanding of all can be developed. In certain cases, such for example as areas reserved for the scientific interests of naturalists and in fact presenting little opportunity for enjoyment by the public at large, the reserve must be kept for scientific purposes if these are to be effectively pursued: in other cases part of a reserve can be set aside for ecological observation, ecological experiment or educational purposes, while the rest is left to the unrestricted use of the public. By means of demonstrations of ecological work it should not be impossible to interest many members of the public in this activity, and in the intimate bearing it has on the proper maintenance of the whole area, to the advantage of all concerned. The opportunities for a widened nature study by school classes are very obvious.

The important point is that there is no real conflict of different interests in the conservation of nature. Each can, and should, help the others, and all that is required to bring about harmony and co-operation is an understanding of the facts and principles involved.

(v) *Scheduled Areas*

'These areas were defined in Conference Memorandum No. 1 (p. 2) as "areas in which further development would be prohibited or drastically restricted. In these the existing movement of the public would in no way be interfered with"...any question of acquiring the land or interfering with its present usage or ownership would not arise. The only requisite for the preservation of their natural interest and amenity value is that they should be protected as far as possible from destructive changes'. (N.R.I.C. Report, par. 14).

'If such areas were carefully selected, many could be made to fulfil within themselves and by the simplest means all the three purposes of nature conservation...and they would certainly secure in a most satisfactory manner the preservation of many types of plant and animal community of the greatest importance for the advancement of scientific or economic studies. These areas would vary greatly in shape and size. The method might for instance be satisfactorily applied to saving some of the as yet undeveloped parts of the coast-line and such areas as the Norfolk Broads. Other sites which might be so chosen contain villages and even small towns and are extensively cultivated. Here it would be necessary to impose some restriction, or at least a carefully planned control, on further building and perhaps in other ways' (par. 15).

'It is suggested that such areas should be zoned in the relevant Planning Scheme for protection as Rural Zones or sometimes as "Private Open Spaces" or in some other instances as "Agricultural Land".'

'There are many areas of land in rural districts, containing communities of flora and fauna of scientific interest, which it may be felt unnecessary to

acquire as nature reserves, so long as the land is adequately protected from development. If any such land is scheduled under the most suitable of the categories indicated it will be safe, unless and until the Planning Authority subsequently make an Order, with the approval of the Ministry, declaring the land no longer reserved....Where areas have been scheduled in Planning Schemes for preservation... with the object of protecting their scientific interest, no subsequent Order varying the use of such land should be made except with the consent of, or at least in consultation with, the National Reserves Authority' (par. 50).

Your Committee is in cordial agreement with these proposals. If an adequate number of well-selected areas can be scheduled in this way, so much of rural Britain will be safeguarded as can reasonably be preserved in the face of other imperative national requirements. The outstanding purpose that will be served is the maintenance of a large part of our national heritage of beauty, both that which depends on natural landscape and vegetation and that which owes its character to the rural settlement and agriculture of the past. Incidentally, as it were, many sites of great interest to the ecologist will be preserved, whether they are made specific Nature Reserves or not.

The scheduling of extensive areas will require great care if on the one hand large samples of the most important and characteristic tracts of country are to be preserved and on the other hand existing legitimate interests are not to be unduly interfered with. Much will depend on the ultimate Government decision as to the conditions of land ownership, and on the issue of the conflict between purely economic interests and the imponderable but vitally important value of preserving the country from defacement. Apart from areas scheduled for the sake of maintaining a mainly agricultural countryside, there are five main types of country in the regions east and south of the midlands which depend for their character largely on natural and semi-natural vegetation and are of the greatest importance. First, there are the still unspoiled parts of the coastline, including sand dunes and shingle beaches, salt marshes, cliffs and undercliffs. The importance of these is widely recognized. Secondly, there is the chalk country with its downland pasture, scrub and woodland, including the characteristic and specially beautiful beechwoods. There should be at least one scheduled area on the South Downs, one on the North Downs, at least one on the western chalk area (Hants, Wilts, Dorset and Berks) and one on the Chiltern Hills. Thirdly, there is the heathland, some of it of little or no value to agriculture, but unfortunately, from the point of view of rural preservation, very suitable for new building estates. Several areas including wide stretches of heath should be scheduled—in East Anglia, in the south-eastern counties, and in Dorset. Fourthly, there are the extensive tracts of country on clays and loams, as in the Weald, which support many deciduous woods, largely oakwoods in 'coppice with standards', alternating with man-made grassland. Fifthly, there is the area of the Norfolk Broads, which includes the only remaining considerable area of unspoiled fenland in Britain. The total square mileage of this fenland is not large, since it is confined to the comparatively narrow river valleys of the Bure, Yare and Waveney and their small tributaries, but it is of unique importance both for public amenity and for ecological interest. Thousands of people annually find pleasure and healthy exercise in sailing, rowing and fishing on the broads and rivers, and the adjoining unspoiled fenland forms a large part of the natural background of their enjoyment. The undrained or partly drained fenland, with the aquatic flora and fauna of the broads and rivers themselves, is of the highest interest to ecologists, and there are many problems connected with it awaiting ecological investigation, besides many local species that should be preserved. Some of the natural woods of alder, birch and other trees and shrubs that have sprung up on parts of these fens are among the very few practically virgin woods remaining in Britain. If it cannot be made a National Park, this whole fenland area should at least be scheduled against destructive changes, and there should be one or more National Nature Reserves established within it.

In the west and north of the country there are many areas of importance, and the choice is much larger, for there is a much greater extent of uncultivated land. There are, however, some areas of outstanding importance which will doubtless receive attention from the local subcommittees of the N.R.I.C.

(vi) *Administration of Nature Reserves*

(*a*) *National Reserves*

Under this head, as we have seen, the N.R.I.C. would recognize only Habitat and Species Reserves, and they would wish to see established a central National Reserves Authority 'having equal and parallel status within its own field with that of the National Parks Authority', which, it is assumed, would control the National Parks (par. 32). 'The necessity for a single central body with full executive responsibility over the selection, acquisition, control and management of all National Reserves' is emphasized, and it is also laid down that 'the technical complexity of the problem of control and management, as well as that of selection, makes it imperative that the executive authority should be composed of persons having expert knowledge of plants and animals and their natural communities, but they should have the assistance of such administrative officers as may prove necessary. Such

a body, though having executive powers in relation to National Reserves, should be available to act in an advisory capacity to the National Parks Authority as well as to those concerned with the control and management of Local Reserves, Scheduled Areas and lands owned by public bodies, and arrangements should be made for the maintenance of a close liaison between the various authorities concerned' (par. 33). With the general purport of these recommendations your Committee is in full agreement.

The N.R.I.C. further recommend that the actual administration of the National Reserves should be carried out by dividing the country 'into a suitable number of Conservancies, each under a Conservator who would have under him an adequate staff of Wardens. The Conservators would be responsible to one or more Senior Conservators, who would be charged with general supervision, and would be the link between the local officers and the National Reserves Authority. Appointments to the posts of Conservators and Senior Conservators would require careful selection, as these officers would need to combine the specialized knowledge of competent field naturalists with practical ability in the management of land' (par. 37).

Some such machinery as that proposed would certainly be necessary, but it should, in the opinion of your Committee, form part of a wider scheme for a Wild Life Service such as is suggested on pp. 20 and 21 of this Report.

(*b*) *Local Reserves*

'Since the primary function of this type of reserve is the preservation of sites of local, scientific, amenity and educational value, their selection, acquisition, control and management should be a matter for voluntary effort by individuals, societies and other bodies that have these interests at heart. In this field local authorities, and more particularly County Councils, have a large sphere of interest. County Councils and County Borough Councils are directly concerned in the educational and indeed in the general amenity value of nature reserves.

'The Committee therefore recommend that the powers of local authorities should be enlarged so as to enable them to purchase or contribute towards the cost of the purchase of, and to maintain, or contribute towards the cost of maintenance of, nature reserves within or without their respective areas, and whether or not such reserves are intended to be vested in them. Planning authorities also should be enabled to secure the preservation of such reserves under their Planning Schemes' (par. 40).

'The holding authority for Local Reserves may reasonably vary with the individual circumstances of acquisition. Where the purchase money and cost of upkeep are met by voluntary effort or by the County Council it may be desired to vest the reserve in the Society for the Promotion of Nature Reserves, in County Councils, or in similar bodies' (par. 42). 'Certain Local Reserves may well remain in private ownership and even under private management, but in this event some agreement should be come to between the landowner and the local body directly concerned with the continued preservation of the site. When a landowner is able and willing to bind himself and his successors in title to maintain an area selected as a Local Reserve, the agreement should if possible be made effective and binding by provisions inserted in the relevant Planning Scheme or by deed of covenant between the parties directly concerned.... It would be most desirable to secure that all reserves remaining under private management should be open to qualified scientific inspection at reasonable periods and that the owner should undertake to allow that degree of public access which would be compatible with the proper maintenance of the reserve' (par. 43).

'In the selection of the reserves and in the delimitation of their boundaries great care would have to be exercised either to include a sufficiently wide belt of land round the actual site to be protected or to secure such control over the uses of this belt as would safeguard the site from many deleterious marginal effects. The advice of the central National Reserve Authority should invariably be sought on all questions of selection and delimitation of Local Reserves' (par. 44).

'A number of existing nature reserves are controlled and managed by local committees. This method is probably that most suitable for the Local Reserves here contemplated. The nature and the constitution of these committees would depend upon the manner in which the reserve was held, but in any event it would be desirable to secure that the County Council in whose area the reserve was situate should be represented upon them. Other obvious persons would be representatives of local, and even perhaps national, societies, and naturalists with knowledge of local conditions. The appointment and duties of conservators or wardens would be a matter for consideration by the committee of management. These committees might well control a group of Local Reserves, and where educational reserves were included, representatives of the institutions likely to make use of them should be appointed for service on these committees.

'Care should be taken to ensure that adequate scientific advice is available and is followed. The obvious body to supply such advice would be the National Reserves Authority, and their Conservators in the area should be responsible for maintaining the closest touch with these managing bodies' (par. 45).

'Local authorities should be empowered not only to acquire and hold reserves but also to make and enforce bye-laws for the prevention of nuisance and damage and for the preservation of order. It is

further recommended that Nature Reserves shall be included in matters to be dealt with in Planning Schemes' (par. 46).

Your Committee is in general agreement with the proposals in regard to Local Reserves contained in the foregoing paragraphs quoted from the N.R.I.C. Report, but would add the following considerations.

As we have already argued (p. 16) there is not only no valid reason why the majority of reserves should not be used for all three of the purposes for which reserves may be made, but there are great positive advantages in so using them. For this reason it is desirable that the local committees of management should usually include representatives of all three interests, i.e. members of public bodies, teachers, and naturalists, including ecologists. By their association on the committees these different types of member would learn to understand one another's interests and the ways in which each interest could be helpful to the others. Among teachers, members of the biological staffs of local universities or university colleges should certainly be included wherever possible, for they would combine the scientific and the educational interests.

It is true that there is often a single dominant motive in the proposal to make any particular reserve, which may be either intended primarily for public enjoyment or for the preservation of a particular type of wild life. In most cases these different uses need not conflict and may, on the contrary, be made to serve one another. But there are of course reserves where the effective preservation of wild life does preclude unlimited public access, and there are others suitable for public enjoyment but containing little of ecological interest. Furthermore, there are some Species Reserves where secrecy is necessary in order to prevent the depredations of unscrupulous collectors. The existence of this small minority of exceptional cases should not hinder recognition of the possibility and desirability of using most reserves for more than one purpose, even though it was originally proposed with a single end in view.

In the opinion of your Committee it is desirable that the National Reserves Authority or other central Government authority charged with the conservation of wild life (see pp. 20–21) should keep a record with full particulars of all reserves, local as well as national, which included among their objects the preservation of any kind of wild life. The Local Reserves, as is pointed out in the N.R.I.C. Report, will supplement the National Reserves in an important way, and the whole should form a system of reservation illustrating the nature and distribution of native plant and animal life. Particulars of the whole system should be published in a suitable form so as to be available to naturalists and the interested public.

6. THE NEED FOR AN EDUCATIONAL CAMPAIGN

Appreciation of the character and beauty of unspoiled country is widespread, but it is far from being universal. Interest in natural history, outside the ranks of professional naturalists, is also widely diffused, though it is perhaps true that its hold has diminished in some parts of the population during the past half-century.* There is probably a smaller proportion of country parsons who are naturalists to-day than at the end of last century, and the same seems to be true of working men in the north of England. Many local natural history societies are seriously weakened and others have disappeared. The causes are probably the multiplication of other interests and the greatly increased pace of modern life.

Nevertheless, it seems to your Committee that there is now a greater potential field for the development of both these interests than ever before. Owing to the development of motor traffic large numbers of town dwellers are able to visit the country more frequently and to range much farther. The need of change and refreshment that can be had in this way is more keenly felt just because of the strain of modern town life, while appreciation of natural beauty and interest in natural scenery and wild life can greatly intensify the pleasures and benefits of country excursions and sojourns.

A more widespread knowledge and understanding of the different natural types of country, their physical features and their characteristic vegetation are just what is required to build up a discriminating appreciation of rural beauty and enthusiasm for its preservation. This of course includes the farmlands which occupy most of our lowlands as well as the areas which still bear natural or semi-natural vegetation. If means can be devised of effectively spreading this sort of knowledge, the repercussions should contribute in an important way to the success of schemes for nature conservation. If sufficient people are fond enough of unspoiled country and would hate to see it disappear, their voices will gain an effective hearing.

There are several ways in which such knowledge could be disseminated, and the following may be suggested.

(1) The preparation of a series of attractive illustrated regional booklets dealing in the first place with favourite routes for trips by motor coach and private car from centres of population, later with more remote areas. Each booklet should deal with the physical features, geology, soils, natural vegeta-

* An exception is the recent vigorous growth of interest in our native birds, of which the great increase of bird watching and bird photography and the immense success of the Royal Society for the Protection of Birds are strong evidence.

tion and agricultural use of the area, together with the towns and villages, all of course in strictly untechnical language. Attention should be specially drawn to beautiful and characteristic features of all kinds. Brief historical remarks should be introduced and current or probable future trends of development noted. The characteristics of 'beauty spots', which are often the goals of motor trips, should be fully described, and the opportunity taken to introduce anti-litter propaganda and to discourage the defacement of nature, for instance by wholesale and indiscriminate plucking of flowers and branches and the uprooting of plants. Any existing Nature Reserves in the region, and their purposes, should be mentioned, except in the case of those Species Reserves in regard to which it is desirable to maintain secrecy.

If such booklets were skilfully written from full knowledge, in a simple attractive style, avoiding technicalities and also all tendency to 'write down' to the reader, they should have a very good sale and a gradual but powerful educational influence. Much can be said for making them official publications, as are the bulletins and circulars of the 'Fish and Wildlife Service' of the U.S. Department of the Interior; but alternatively the scheme should be attractive to publishers.

(2) Nature Reserves, both National and Local, except those which are unsuitable for the purpose, should be made centres of education in field natural history. A large part of the public support that can be gained for nature conservation must arise from the stimulation of local interest in local country and its vegetation and animal life. Demonstrations of the nature and character of unspoiled samples such as are set apart as nature reserves will be the best means of arousing interest. To these should be added explanations and demonstrations of the effects of various kinds of human activity on similar country which can be seen in the same neighbourhood. Interest should be primarily directed to types of natural and semi-natural vegetation, the plants of which they are composed, and the changes they undergo, both when let alone and when subjected to various treatments, e.g. the pasturing of grassland, the burning of heaths, etc.: for it is upon the vegetation and its changes that the character of British scenery mainly depends.

In this educational function of reserves local schools could take a great part. Members of the biological staffs of local universities, where such institutions exist in the neighbourhood, would certainly be willing to help, and so would local natural history societies.

(3) Descriptions of the different reserves should be prepared in pamphlet form and should be available for sale at the reserve. They should be more detailed and thorough than the booklets proposed under (1), but at the same time easily understood by non-specialists, though with more than a purely popular appeal. These pamphlets would serve as handbooks to the reserves for all who used them, including the schools. Those relating to the National Reserves would be official publications.

(4) Lectures and field trips should be organized in connexion with the reserves by competent naturalists, whether members of university staffs, schoolmasters, members of local natural history societies or others.

7. THE ESTABLISHMENT OF A NATIONAL WILD LIFE SERVICE

The concluding words of the N.R.I.C. Report (par. 52 and Summary, par. xlv) are these: 'The Government should take formal responsibility for the conservation of native wild life, both plant and animal.'

Your Committee heartily welcomes this declaration which they believe to be the key to the success of any comprehensive scheme of conservation. What is wanted is first of all unequivocal public recognition of nature conservation as a national interest, implemented by a national scheme and supplemented by local effort.

The establishment of a series of National Nature Reserve is an indispensable and invaluable step, but alone it is not enough. As we have seen, Nature Reserves are not by themselves sufficient to conserve our native birds and mammals. What is required is continuous study of the distribution, density and habits of each species and of the interrelationships between them, not only those of predator and prey but many others. Such study is both a scientific and an economic interest, as is shown by the very successful work of the Bureau of Animal Population at Oxford, particularly with the small rodents. The 'control' of pests, it has been well said, is the mirror image of conservation. Exactly the same type of knowledge is required for one as for the other. Control in the proper sense, i.e. regulation, is what must be aimed at, and scientifically acquired knowledge is its essential prerequisite. In order to gain and apply such knowledge on a sufficiently comprehensive scale a national service is necessary.

But it is not only the problems of birds and mammals which are involved. Invertebrate animals and plants present a host of problems, all of great scientific interest, and many of economic importance as well. A National Wild Life Service which would be an effective organ of nature conservation should embrace the whole field of the native flora and fauna, and only in this way we believe can a really successful scheme of nature conservation be established. We have an example in the American 'Fish and Wildlife Service' of the Department of the Interior, though this does not include plants and invertebrates. There would be great advantage in making the British scheme comprehensive of all wild life because the whole forms a great web with the most

complex interrelations between its different strands, and increased knowledge of parts of this web is continually throwing light on other parts.

In such a service the National Nature Reserves would play an important part, for they would be natural centres of observation and experiment. Experimental use would in no way interfere with conservational and educational functions. Only small portions would be used for experiments calculated to change the vegetation or animal population, so that the aesthetic aspects of the whole reserve would not be affected. And the carrying on of experiments in a reserve would actually enhance their educational value. The same sort of work could be carried on in Local Reserves, but subject of course to the approval of the local committees of management.

Part of the work of a Wild Life Service would be the National Nature Reserves, the function of the Conservators under the N.R.I.C. scheme. Conservators and Wardens of National Reserves would indeed be officers of the Service. But continuous research on the problems of conservation and control, whether within or outside the reserves, would be an essential part of the duties of the Service, and these problems, as we have seen, are always, at bottom, ecological problems. A considerable degree of specialization would be necessary, for the habits and density of a population of mammals or birds, for example, is a very different subject from the control of the plant population of a reserve. But a thorough general acquaintance with natural history in the field would be the proper foundation of the training of all officers, who should always be alive to possible interrelations, which are often unsuspected and subtle, between organisms of widely different types.

It is suggested that it would be preferable to constitute the central authority of a Wild Life Service as a separate body under the Privy Council, with a status similar to that of the Medical Research Council, and to make the selection and supervision of National Nature Reserves part of its work, rather than to set up a National Reserves Authority parallel with the National Parks Authority and to place it under the Ministry of Town and Country Planning, as the N.R.I.C. Report proposes, or under any other existing Ministry. It would be well to keep the Service independent of the policy of a Ministry with different primary purposes and to enable it to create its own policy and traditions.

SUMMARY

1. Despite the immense change in the face of the country from its original condition there remain considerable tracts covered by wild vegetation with the multitudes of lower animals it harbours. Though the larger carnivorous mammals have disappeared and the larger predatory birds are greatly reduced, many smaller mammals and a great bird population still exist. The whole of this wild life is part of the national heritage, valuable to the nation in many different ways, and it is threatened with serious and widespread destruction in the immediate future. The means of preserving as much as is compatible with other objects of paramount national importance require careful consideration. The only method of preserving wild vegetation with its population of lower animals is to set aside areas as nature reserves. The higher animals and birds require separate treatment.

2. The first object of nature preservation, which has the widest support, is maintenance of the beauty and interest of characteristic British scenery. In the past this was largely preserved by the existence of large private estates which are probably destined to disappear. Public action is the only alternative means of preventing destructive change. In future 'country planning' rival claims to the use of land, both between different possible economic uses and between these and the preservation of natural scenery, will have to be decided, and give-and-take will be necessary. The scientific claim to the preservation of wild life depends very largely on the modern science of ecology which has important economic as well as purely scientific value, and the ecological interest coincides very largely with the aesthetic and sentimental, because both demand the preservation of considerable tracts of unspoiled vegetation with its accompanying animal life. Education in natural history is not only important in itself, but it enhances appreciation of the natural beauty of landscape, and good education of this sort depends on the advice of ecology. Thus each of these three interests reinforces the others.

3. The problems of nature conservation must be viewed against the human background. The increase of motor transport and the great effectiveness of modern means of destruction press hardly on all kinds of wild life. Such means are largely used to further sectional interests and are constantly 'upsetting the balance of nature'. Just what should be destroyed and what preserved should be a matter of public policy, and the balance aimed at should be the ecological expression of the resultants of the different human desires. The increased attention to forestry with its inevitable replacement of much natural and semi-natural woodland (too often derelict) by economically managed forests and plantations of conifers is discussed at some length as an example of the pursuit, under national authority, of an economic interest which has wide repercussions on nature conservation. It is suggested that a wider policy would enable the Commission to play an important part in the conservation of nature as well as to develop great new forests, provided the whole land surface were available for inclusion in a comprehensive scheme. Game preservation has two opposite effects on wild life. It preserves much natural

vegetation (such as deciduous woods and copses for pheasants, heath, moor and mountain for grouse and red deer), with the animals which inhabit it, so far as these are not inimical to the game itself: on the other hand, predators are ruthlessly destroyed, and this has led to great increases in the numbers of small rodents, which do serious damage to crops and young trees. If all game preserving were to cease and no alternative protection put in its place, we should soon lose most of our existing wild life habitats, at least below an altitude of 1000 or 1500 ft.

Love of nature has probably become more widespread in recent years (though natural history as such has been losing its hold on parts of the population), and a notable instance is the attachment to wild birds. Such sentiments cannot be ignored in country planning but must be considered along with economic interests.

4. (i) The establishment of National Parks and 'Scheduled Areas', though they would safeguard much natural vegetation, cannot meet the whole of the scientific needs. Many smaller areas (Nature Reserves) under management primarily designed to meet these needs are required. It is proposed by the semi-official Nature Reserves Investigation Committee that *National Nature Reserves*, to be acquired by the State and administered by a State authority, representing all the important British types of natural habitat and natural plant community, should be distinguished from *Local Nature Reserves* acquired or held locally under various arrangements with their present owners and used for scientific, educational or 'amenity' purposes. Informed and careful scientific management is necessary for nearly all reserves. Most areas which would be reserved depend for part of their character on human activity in the past and present, and it is necessary that this activity should be continued or replaced by other means if their character, on which the whole value of the areas depend, is to be retained. Areas which have always been immune or nearly immune from human interference are few, but naturally of great ecological importance. In general they require less active management than the semi-natural areas. But the great majority of reserves require expert management. Though the primary functions of National Parks are different, and their administration will properly be entrusted to a separate authority, yet the maintenance of their natural vegetation must always be a primary object if their beauty is to be preserved, and to achieve this expert advice will constantly be necessary. Much of the knowledge required has been gained through the ecological work of recent years, and this will be constantly added to as fresh research is undertaken. National and Local Nature Reserves will afford exceptionally good opportunities for such research.

(ii) Invertebrate animals such as molluscs, insects and other groups are automatically protected if the vegetation they inhabit remains undisturbed. Particular tracts of vegetation known to harbour rare species should be reserved and the activities of collectors restricted.

(iii) The further diminution of fresh-water pollution is the most important measure that can be taken for the conservation of fish populations, and this is already strongly supported by the powerful angling interests. Reservation of particular ponds and small lakes for the sake of their plant life, water birds, etc., may no doubt reduce or destroy the water as a habitat for fish, but the number of reserves required for such purposes is quite limited, and in some cases appropriate management could provide for both interests.

(iv) Most of the twelve native species of amphibia and reptiles are of widespread distribution and in no serious danger, but three species are very local and the areas in which they occur contain in fact very suitable sites for nature reserves (probably National) on several different grounds.

(v) Birds and mammals, both because of their great powers of movement and because certain species directly involve human interests, cannot be conserved simply by reserving particular areas. The problem of conservation involves that of control and always becomes one of attaining and preserving a certain optimum density and distribution of individual species in different parts of the country. This necessitates the application of the results of research to the field problem. (*a*) Proper balancing of various material and cultural claims is a necessary preliminary to a decision on the precise goals of control (in the sense of 'regulation'). Adequate publicity and increase of public knowledge and interest are necessary to obtain popular support for the measures taken. Sectional interests give rise to very different attitudes to different species of animal. Shooting men wish to increase the populations of certain native and introduced game birds and to see those birds and mammals which prey upon them diminished or wiped out. This desire has led to a great scarcity of predators. The fox stands in an exceptional position because it is both a predator and itself an object of sport. The introduced rabbit throughout its long history in this country illustrates the fluctuations and conflicts of human interests. There is a case for allowing the continued existence of moderate and controlled rabbit populations in some areas. There is also a case for maintaining a moderate (rather low) population of the common vole in hill regions, though in excessive numbers it does serious damage to young plantations. The two squirrels (red and grey), endemic races of Hebridean mice, seals on the Cornish coast, and the proposed abolition of hedgerows and small copses in agricultural country provide examples, among many others, of conflicts between real or supposed interests which can only be resolved by control based on a just balancing of the reality and

importance of the different interests. (*b*) Many different animals have been introduced into this country at various times and with various objects. Some of them have done a lot of harm, unconsidered by the introducers. (*c*) The main uses of reserves for vertebrate animals are to protect localized breeding stocks, roosting aggregations of bats, and very local species which have no great powers of movement. Many birds and the larger mammals, which have such powers, cannot be safeguarded in reserves. General control is required and this must be based on accurate knowledge of the habits of the different species, knowledge which can only be obtained by research.

(vi) All naturalists have an interest in prevention of the extinction of rare species. 'Sanctuaries' or—better—'Species Reserves' for this purpose must, however, be examples of the particular community in which the species naturally occurs, and while the occurrence of the particular species adds to its interest the choice of sample communities for preservation cannot be limited on that ground.

5. Haphazard procedure in nature reservation, valuable as it has been in the past, now requires to be replaced by a systematic and comprehensive plan of national scope.

(i) The N.R.I.C. propose that a series of *National Nature Reserves* should be made, selected and managed so as to ensure the survival of all the main natural and semi-natural communities of plants and animals for the purpose of serious study. The location of these must depend on the natural distribution of the communities in question, their management must be expert and subjected to unified direction with full responsibility at the centre. This proposal has the complete support of your Committee.

(ii) The type of reserve described in (i) is called by the N.R.I.C. a 'Habitat Reserve'. Besides this they propose the establishment of 'Species Reserves', some of which would be National Reserves and which are intended to secure the survival of rare or very local species. Since it is admitted that a Species Reserves would really be a Habitat Reserve which contained one or more rare species, and would require exactly the same kind of management, it would seem unnecessary to draw a sharp distinction between the two. It would seem sufficient to select certain Habitat Reserves not only because they contained good examples of natural communities but also because they contained rare species—a course all naturalists would desire. A reserve made on these grounds should always be much larger than the area occupied by the rare species, to allow room for possible expansion of occupied area, or shift of the species. It is always the habitat, as the essential condition of the continued existence of the species, which it is important to safeguard.

(iii) The 'Amenity' and 'Educational' Reserves contemplated by the N.R.I.C. since they 'subserve local rather than national needs' are placed under the category of *Local Nature Reserves*. Your Committee wishes to stress the point that most, though not quite all, nature reserves, national as well as local, can fulfil all three functions of a reserve—scientific, educational, and 'amenity'—without damage to any, and that it is most desirable that all which can should be made to do so, because in this way they will serve the widest range of interest and obtain the greatest measure of public support. The general conclusion seems to be that all nature reserves must really be 'habitat reserves', and that the maintenance of their threefold value depends essentially on ecologically instructed management, which is alone competent to decide what can be permitted and what disallowed in the conditions of particular reserves.

(iv) Scattered through the country there is already a considerable number of reserves which have been made for diverse purposes, and many of them are vested in the National Trust. Most of these have been made with the object of securing to the public the use and enjoyment of areas of natural beauty, but in some of them conditions permit of scientific work within the reserve. A few belong to the Society for the Promotion of Nature Reserves, and these are selected because they are of interest to naturalists. Besides these there are others belonging to local societies, trusts or private individuals. Such reservations will no doubt continue to be made whether a national scheme is adopted or not, and since they will usually be made mainly by local effort their ownership and administration must naturally be determined by local wishes. As in the case of National Reserves, it seems unnecessary to divide Local Reserves into rigid categories, since many of them can be so well employed for more than one purpose, and where possible it is highly desirable that the different functions should be carried on side by side. An exception must be made in the case of those reserves intended to promote the interests of naturalists and in fact unsuitable for the enjoyment of public amenities. But usually the various interests can be harmonized by enlightened management, sometimes by setting aside part of the reserve for scientific work and allowing the public free access to the rest.

(v) The proposal by the N.R.I.C. to schedule certain areas in which further development would be prohibited or drastically restricted, without interfering in any way with the present use of the land or the existing free movement of the public, is warmly welcomed by your Committee. If an adequate number of well-selected areas are thus scheduled, a large part of our national heritage of beauty will be maintained, both that which depends on natural landscape and that which owes its character to rural settlement and agriculture. Incidentally, as it were, many sites of great interest and importance to the ecologist will be preserved, apart from the formation of specific nature reserves. It is suggested that in southern and

eastern England there are five main types of country of which large areas should be scheduled: (1) parts of the coastline that are still unspoiled, with their sand dunes, salt marshes and cliffs, (2) the chalk country with its downland and beechwood, (3) heathland, (4) clayland bearing coppices with oak standards and grassland, and (5) the river valleys of East Norfolk with their rivers, broads and still unspoiled fenland.

(vi) (*a*) The N.R.I.C. recommends the establishment of a central National Reserves Authority having full executive responsibility over the control and management of all National Nature Reserves and composed of persons having expert knowledge of plants and animals and their natural communities. It should be available to act in an advisory capacity to the National Parks Authority as well as to those concerned with the control and management of Local Reserves, Scheduled Areas, and lands owned by public bodies. With these recommendations your Committee is in general agreement. The N.R.I.C. further recommends that the National Reserves should be administered by Conservators (with Wardens under them), and one or more Senior Conservators who would be the link between the Conservators and the National Reserves Authority. The qualifications of the Conservators and Senior Conservators would have to combine the specialized knowledge of competent field naturalists with practical ability in the management of land. Some such machinery as that proposed would certainly be necessary, but your Committee is of opinion that it should form part of a wider scheme of the nature of a 'Wild Life Service' (see Section 7).

(*b*) The N.R.I.C. makes a number of detailed recommendations about the selection and classification of Local Nature Reserves, their tenure, management by local committees, the representation of various interests on these committees, and the necessity of advice from the National Reserves Authority. With these your Committee is in general agreement, but would suggest that since many nature reserves can and should be used for all three purposes —scientific, educational and public enjoyment—it is desirable that the local committees of all such reserves should include representatives of the three interests, who would by their association on the committee learn to understand one another's interests and the ways in which each interest could be helpful to the others. Wherever possible members of the biological staffs of local Universities and University Colleges should be included, as these would combine scientific and educational interests. Your Committee is of opinion that the National Reserves Authority or other central authority charged with the conservation of wild life should keep records with full particulars of all reserves, local as well as national, which included among their objects the preservation of any kind of wild life, and should make them available to naturalists and the interested public by appropriate publications.

6. It seems to your Committee that there is now a greater potential field for the development of appreciation of the character and beauty of unspoiled country and of interest in natural history than ever before. A more widespread knowledge and understanding of the different natural types of country, of their physical features and their vegetation, is just what is required to build up a discriminating appreciation of rural beauty and enthusiasm for its preservation, and an educational campaign is necessary. The repercussions should contribute in an important degree to the success of schemes for nature conservation. Such an educational campaign could be promoted in several ways, e.g. by the preparation of a series of attractive popular illustrated booklets dealing with the physical features, geology, soils, natural vegetation and agricultural uses of the country on popular motor routes from centres of population; by making suitable Nature Reserves, both National and Local, centres of education in field natural history, thus stimulating local interest in local country and its vegetation and animal life; by publishing untechnical but thorough descriptions of the different reserves in pamphlet form to be purchasable at the reserve; by organizing lectures and field trips conducted by competent naturalists in connexion with the different reserves.

7. 'The Government should take formal responsibility for the conservation of native wild life, both plant and animal.' These concluding words of the N.R.I.C. Report are warmly welcomed by your Committee, which believes that they contain the key to the success of any comprehensive scheme of conservation. In such a scheme the establishment of a series of National Nature Reserves is an indispensable and invaluable step, but by itself it is not enough. Nature Reserves are not sufficient to conserve our native birds and mammals. What is wanted is continuous study of the distribution, density and habits of each species and of the relationships between them. Such study is both a scientific and an economic interest. What can be done in this field is shown by the work of the Bureau of Animal Population, especially on small rodents, and of the Edward Grey Institute of Ornithology at Oxford. Control of pests in the mirror image of conservation. Exactly the same kind of knowledge is required for one as for the other. In order to gain such knowledge on a sufficiently comprehensive scale a national service is required. It is not only the problems of birds and mammals which are involved. Invertebrate animals and plants present a host of problems, all of great scientific interest and many of economic importance as well. We need only refer to insect and fungal pests and their host plants and animals. There is a great deal to be said for establishing a National Wild Life Service to embrace the whole flora and

fauna, and such a service we believe is necessary if we are to have a really effective organ of nature conservation. In such a service the National Nature Reserves would play an important part, for they would be natural centres of observation and experiment, and these need in no way interfere with their conservational functions, since experiments calculated to change their aspect would be restricted to small parts of the reserve. The educational function would actually gain by such work. Conservators and Wardens of the National Reserves would be officers of the proposed Service. But whether they themselves could undertake it or not, continuous scientific research on the problems underlying practical conservation and control would be an essential function of the Service.

It is suggested that it might be preferable to constitute the central authority of a Wild Life Service as an independent body under the Privy Council, with a status similar to that of the Medical Research Council, rather than assign it to the Ministry of Town and Country Planning or any other existing Ministry.

GENERAL CONCLUSIONS

Your Committee considers that the *Report of the Nature Reserves Investigation Committee* is a very valuable document. With most of the considerations and recommendations of that Report they are in close agreement.

They particularly welcome the claim that 'the Government should take formal responsibility for the conservation of native wild life, both plant and animal', and the recommendation that a number of National Nature Reserves, representing all the important types of British vegetation with accompanying animals, should be acquired by the State and placed under a central State Authority with expert personnel; while the continued acquirement locally of Local Nature Reserves to supplement the National Reserves should be encouraged and advice from the Central Authority on their management should be freely available. They also welcome the suggestion to 'schedule' typical areas in which destructive 'development' would be prohibited.

Your Committee would, however, suggest that the division of Reserves proposed by the N.R.I.C. into Habitat, Species, Amenity, and Educational Reserves should not be sharply defined and rigorously carried out. In the majority of Reserves, both national and local, the functions of maintaining the wild life for scientific study, of using it for educational purposes, and for the enjoyment of its 'amenities' can be carried on side by side with great reciprocal advantages, each interest helping the others. The essential condition, however, is the careful regulation of these various activities by expert management. There are also certain reserves in which one of them would have to be made paramount, with limitation or possible exclusion, temporary or permanent, of the others.

Further, your Committee would point out that some of our animal wild life, more particularly birds and mammals, cannot be conserved by means of reserves alone, but requires careful regulation of the densities of the populations of the different species, for which continuous research into their habits and distribution is essential. For this reason, and in order to promote and increase ecological knowledge, which is important in the national interest, both scientifically and economically, your Committee recommend the establishment of a National Wild Life Service, embracing both plants and animals, whose functions would include continuous research as well as the administration of National Nature Reserves; and they suggest that its governing body should be given an independent position under the Privy Council. Only in this way, it is believed, can Government adequately discharge the responsibility for the conservation of wild life which they are now invited to assume.

ON THE RELATIONSHIP BETWEEN TEMPERATURE AND RATE OF DEVELOPMENT OF INSECTS AT CONSTANT TEMPERATURES

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(With 6 Figures in the Text)

CONTENTS

1. INTRODUCTION

Various mathematical formulae have been used by biologists, from time to time, to express the relationship between temperature and speed of development in insects and other poikilothermic animals. The aim of investigators has been to establish velocity constants which will give a quantitative expression for this relationship. The formula of Van't Hoff, and the associated conception of the summation of temperature, have been used widely; the modified formula introduced by Arrhenius has been used also. In 1926 Bělehrádek proposed an empirical formula in which the thermal coefficient b is used. In 1925 Janisch developed the conception of the catenary curve. The reader is referred to Needham (1931), Uvarov (1931) and Bělehrádek (1935) for reviews of the literature on this subject.

The present writer (1942) used a curve of the form

$$\frac{1}{y}=\frac{K}{1+e^{a-bx}}$$

to describe the trend of acceleration in embryonic development in insects as determined by temperature: $1/y$ represents the reciprocal of the time required for complete development to be achieved at a given temperature x: K, a and b are constants. The formula represents a form of the logistic curve developed by Pearl & Reed (1920). Its usefulness in quantitative biology has been shown by several authors, including Lotka (1925), Gause & Alpatov (1931), and Davidson (1938, 1942). In the present paper, a detailed analysis is given of data on the time required for the development of the egg and pupal stages of *Drosophila melanogaster* at constant temperatures, in order to illustrate the way in which the formula is calculated. In addition, the essential data relating temperature to embryonic development are given for five other species of insects, in order to demonstrate further the application of the above formula.

2. DEVELOPMENT OF THE EGGS OF *DROSOPHILA MELANOGASTER*

Powsner (1935) carried out experiments on the development of the eggs of *Drosophila melanogaster* at constant temperatures, with the object of testing the various theories which had been put forward to explain the effect of temperature on the rate of development of insects. The data are, therefore, particularly appropriate for illustrating the way in which the logistic curve can be used in the analysis of data on temperature and development in insects. The relevant data taken from Table 8 in Powsner's paper, are given in Table 1. Certain aspects of the data are discussed in an earlier paper (Davidson, 1942). The eggs were laid at 25° C. and transferred to the stated temperatures within half an hour of

being laid. The number of hours given in column 2 represent the time taken, from oviposition to hatching, for the eggs to develop at the stated temperatures. Powsner adjusted the figures to allow for the small amount of development of the eggs during the short period that they were at 25° C., before being transferred to the particular temperature of the experiment.

Table 1. *Time, in hours, taken by the eggs of* Drosophila melanogaster *to develop completely and hatch at the given constant temperatures*

Temp. ° C.	Time in hours	Reciprocals $1/y$
14·95	67·9	0·014728
16·16	57·6	0·017361
16·19	56·3	0·017762
17·15	48·7	0·020534
18·20	41·4	0·024155
19·08	38·01	0·026309
20·07	33·44	0·029904
22·14	26·54	0·037679
23·27	24·28	0·041186
24·09	22·46	0·044523
24·81	21·14	0·047304
24·84	21·05	0·047506
25·06	20·39	0·049044
25·06	20·41	0·048996
25·80	19·44	0·051440
26·92	18·75	0·053333
27·68	17·76	0·056306
28·89	17·36	0·057604
28·96	17·26	0·058038
29·00	17·14	0·058343
30·05	16·77	0·059630
30·80	16·94	0·059032
32·00	18·17	0·055036

(A) *The temperature-velocity curve*

The observed data in Table 1 are presented graphically in Fig. 1. The closed circles represent the points obtained when time (y) is plotted against temperature (x), so that the distribution of these points indicates the course of the temperature-time curve. The open circles represent the points obtained when the reciprocals for time ($1/y$) are plotted against temperature (x): each of the reciprocals is multiplied by 100, so that values on the ordinate ($100/y$) represent the average percentage development made by the embryos per hour, at the given temperature. Therefore, the distribution of the points indicates the course of the temperature-velocity curve. The speed of development of the eggs increases as the temperature rises, until about 30° C. is reached. Above this temperature, the speed of development decreases rapidly as the temperature rises, until about 33° C. At this latter temperature, the embryo is unable to develop to completion and hatch.

The writer (1942) has defined the temperature at which the embryo develops at the fastest rate, as the peak temperature. This temperature value was not accurately determined in the case of the eggs of *D. melanogaster*: it lies between 29·00 and 30·05° C., and may be taken tentatively as 29·5° C.

The distribution of the 23 observed points plotted in Fig. 1, shows that the temperature-velocity curve follows an S-shaped course, which exhibits a marked change in direction about the peak temperature (29·5° C.). The writer (1942) discussed the reasons why data on the rate of development at temperatures above the peak should not be included when calculating the formula for the temperature-velocity curve.

The 21 observed values for $100/y$ at temperatures between 14·95 and 30·05° C. (Table 1), have been fitted to a curve having the formula

$$\frac{100}{y}=\frac{K}{1+e^{a-bx}}.$$

This is a bisymmetrical, sigmoid curve, the point of inflexion being at $x=a/b$, $100/y=\frac{1}{2}K$.

K is the parameter representing the distance between the upper and lower asymptote of the curve: since the lower asymptote is zero in this instance, K represents the value of the upper asymptote of the curve.

a is the parameter which indicates the relative position of the origin of the curve on the abscissa: if $a=0$, the origin of the curve on the temperature axis will be at $x=a/b$, which is the temperature value at the point of inflexion of the curve, so that the formula then has the simplified form

$$\frac{100}{y}=\frac{K}{1+e^{-bx}}.$$

b is the parameter representing the degree of acceleration of development of the eggs in relation to temperature: it therefore determines the slope and course of the curve.

e is the base of the Napierian system of logarithms.

x is the given temperature.

(1) *How to determine the value of the parameter K*

If the observed points are distributed over the complete course of the projected logistic curve, the value of K can generally be assessed by inspection. In the case of the data we are considering, it cannot be assessed in this way, because the observed points do not extend far enough along the upper portion of the curve (Fig. 1). It can be calculated from the following formula:

$$K=\frac{2P_1P_2P_3-P_2^2(P_1+P_3)}{P_1P_3-P_2^2}$$

where P_1, P_2 and P_3 are values for $100/y$ on the curve at three equally spaced temperatures on the

abscissa.* When observed values for $100/y$ at three appropriate values for x are not available, they are obtained by graphical interpolation.

The following values for P_1, P_2 and P_3 were selected on the proposed curve:

x_1 at 16·18° C., $P_1 = 1{\cdot}7562$,
x_2 at 22·56° C., $P_2 = 3{\cdot}8900$,
x_3 at 28·95° C., $P_3 = 5{\cdot}8000$.

Substituting these values for P in the above formula, the calculated value $K = 7{\cdot}0953$ is obtained.

the course of a bisymmetrical logistic curve. This is evident when the equation of the curve is developed as follows:

$$\frac{K}{1+e^{a-bx}} = P, \quad \frac{K-P}{P} = e^{a-bx}, \quad \log_e \frac{K-P}{P} = a - bx.$$

This is a form of the equation for a straight line.

The 20 values for $\log (K-P)/P$ at 14·95–29·00° C. were fitted to a straight line by the method of least

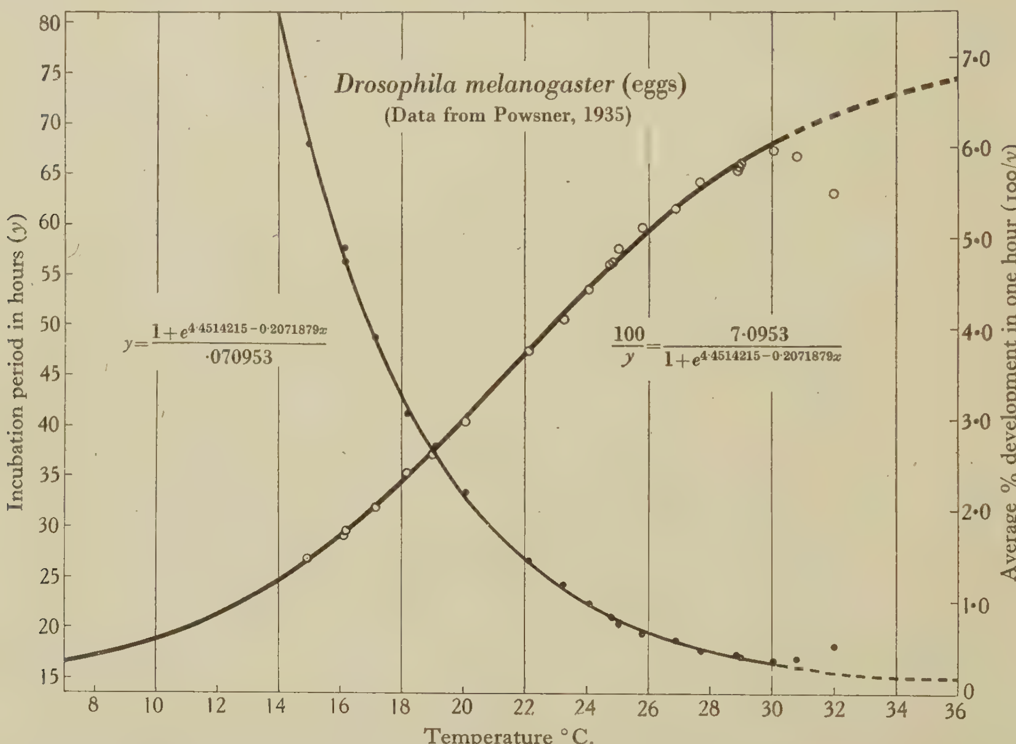

Fig. 1. Observed points on the temperature-time curve (closed circles) and temperature-velocity curve (open circles) for the eggs of *Drosophila melanogaster*. The observed points are plotted from data given in Table 1.

(2) *Linear relationship between* $\log (K-P)/P$ *and temperature*

Values are now calculated for $(K-P)/P$ for each of the observed values of P: they are then converted into common logarithms. When the value of $\log (K-P)/P$, at each of the temperatures 14·95–29·00° C. (Table 2), is plotted against the appropriate temperature, the 20 points approximate closely to a straight line (Fig. 2A). This implies that the distribution of the observed values for $100/y$ in relation to temperature, within this range, follows

* The letter P is used to represent values on the ordinate ($100/y$) because it is more convenient to use a single symbol when forming equations. The reader should note that P represents the same thing as $100/y$, wherever it is used in this paper.

squares. The formula for the line, working in common logarithms, is

$$\log_{10} \frac{K-P}{P} = 1{\cdot}933216 - 0{\cdot}08998x.$$

The observed points approximate closely to the calculated straight line (Fig. 2).

Converting common to Napierian logarithms by multiplying throughout by the factor 2·3026, we obtain the calculated formula for the temperature-velocity curve for the development of the eggs of *D. melanogaster*

$$\frac{100}{y} = \frac{7{\cdot}0953}{1+e^{4\cdot4514215-0\cdot2071879x}}.$$

The curve describes the trend of the speed of

development of the eggs from the lowest temperature at which complete development to hatching occurs, to the peak temperature (29·5° C.). The curve shown in Fig. 1 has been calculated from this formula, the numerical values being given below in Table 2. The values for $100/y$ represent the average percentage development of the eggs of *D. melanogaster*, which takes place per hour at the given temperatures. The 21 observed values for $100/y$ at temperatures ranging from 14·95 to 30·05° C. are a good fit to the calculated curve. The difference between the observed and calculated values (Table 2) shows that the deviation of any of the points from the calculated curve does not exceed 2·15 % of the appropriate calculated value. The greatest deviation is 0·1083 at 25·8° C.: it is 2·15 % of the calculated value. The root-mean-square deviation between the observed and calculated values $\left(\sqrt{\frac{(o-c)^2}{21}}\right)$ is 0·05796, which is 1·15 % of the calculated value at 25·80° C.

(3) *How to calculate the temperature* (x) *for any given value of* $100/y$

When the temperature for a given value of $100/y$ is unknown, it can be calculated from the temperature-velocity curve as follows:

$$\log_e \frac{K-P}{P} = a-bx, \quad x=\frac{1}{b}\left(a-\log_e \frac{K-P}{P}\right).$$

In the case of the eggs of *D. melanogaster*,

$$a=4\cdot4514215; \quad b=0\cdot2071879.$$

(B) *The temperature-time curve*

The formula for the temperature-time curve can be derived from the formula for the temperature-velocity curve:

$$\frac{100}{y}=\frac{K}{1+e^{a-bx}}, \quad \frac{1}{y}=\frac{1}{100}\left(\frac{K}{1+e^{a-bx}}\right).$$

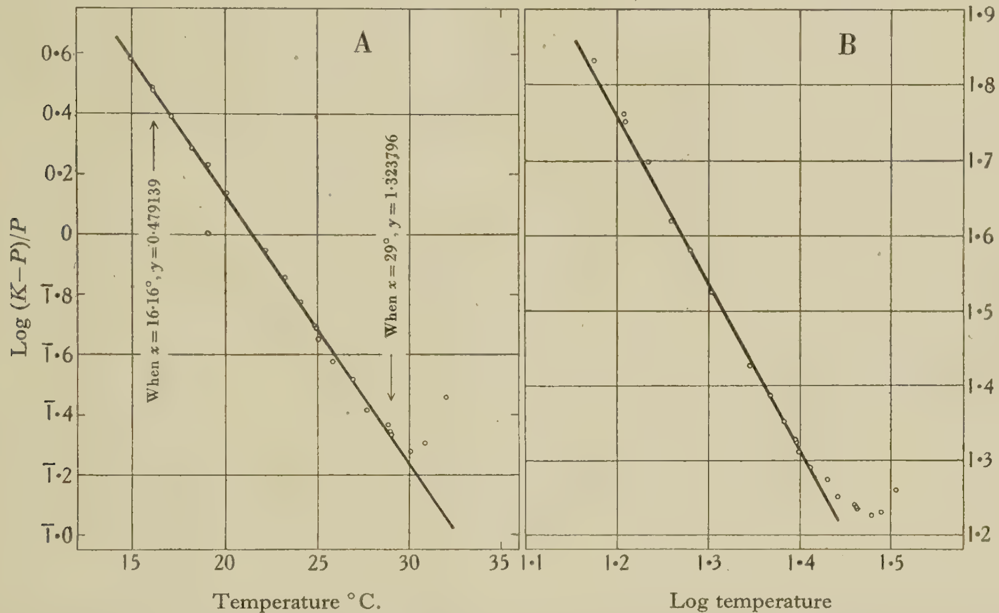

Fig. 2. A, showing the linear relationship between log $(K-P)/P$ and temperature, for the observed values for P given in Table 2. B, showing linear relationship between log time (y) and log temperature (x) according to Bělehrádek's formula.

Table 2. *Showing difference between observed and calculated values for* $100/y$ *at the given temperatures*

Temp. °C.	$100/y$ obs.	$100/y$ calc.	Obs. − calc.
14·95	1·4728	1·4561	+0·0167
16·16	1·7361	1·7666	−0·0305
16·19	1·7762	1·7758	+0·0004
17·15	2·0534	2·0535	−0·0001
18·20	2·4155	2·3849	+0·0306
19·08	2·6309	2·6819	−0·0510
20·07	2·9904	3·0313	−0·0409
22·14	3·7679	3·7880	−0·0201
23·27	4·1186	4·1963	−0·0777
24·09	4·4524	4·4825	−0·0301
24·81	4·7304	4·7235	+0·0069
24·84	4·7506	4·7334	+0·0172
25·06	4·9044	4·8046	+0·0998
25·06	4·8996	4·8046	+0·0950
25·80	5·1440	5·0357	+0·1083
26·92	5·3333	5·3578	−0·0245
27·68	5·6306	5·5560	+0·0746
28·89	5·7604	5·8368	−0·0764
28·96	5·8038	5·8517	−0·0479
29·00	5·8343	5·8602	−0·0259
30·05	5·9630	6·0667	−0·1037

This is the reciprocal form of the temperature-time curve

$$y = \frac{100(1 + e^{a-bx})}{K},$$

in which y represents the time, in hours, required by the eggs of *D. melanogaster* to develop to completion and hatch at given constant temperatures x.

Substituting the appropriate values for the constants K, a and b, the formula for the temperature-time curve becomes

$$y = \frac{1 + e^{4.4514215 - 0.2071879x}}{0.070953}.$$

The curve shown in Fig. 1 has been calculated from this formula. It faithfully describes the trend of the observed values for y at temperatures between 14·95 and 30·05° C. (Table 3). The greatest deviation of any of the observed values from the calculated curve is 0·42 hr. at 25·8° C. which is only 2·1 % of the calculated value at this temperature.

Table 3. *Showing observed and calculated values for the duration of development of the eggs of* D. melanogaster *at the given constant temperatures*

Temp. °C. x	Period (hours) required for development y Obs.	Calc.	Difference obs. − calc.
14·95	67·9	68·67	−0·77
16·16	57·6	56·60	+1·00
16·19	56·3	56·31	−0·01
17·15	48·7	48·70	0·00
18·20	41·4	41·93	−0·53
19·08	38·01	37·29	+0·72
20·07	33·44	32·99	+0·45
22·14	26·54	26·40	+0·14
23·27	24·28	23·83	+0·45
24·09	22·46	22·31	+0·15
24·81	21·14	21·17	−0·03
24·84	21·05	21·12	−0·07
25·06	20·39	20·82	−0·43
25·06	20·41	20·82	−0·41
25·80	19·44	19·86	−0·42
26·92	18·75	18·67	+0·08
27·68	17·76	17·98	−0·22
28·89	17·36	17·13	+0·23
28·96	17·26	17·09	+0·17
29·00	17·14	17·06	+0·08
30·05	16·77	16·48	+0·29

3. DEVELOPMENT OF THE PUPA OF *DROSOPHILA MELANOGASTER*

Ludwig & Cable (1933) carried out experiments to determine the speed of development at constant temperatures of the pupa of *D. melanogaster*. The insects were allowed to develop to the pupal stage at 25° C.: the pupae were then removed to the experimental temperature, within 1 hr. from the commencement of pupation. Observations at the time of emergence of the flies from the pupal cases were made hourly, except at 15° C.; at the latter temperature the observations were made at intervals of about 8 hr. Records were kept of the sex of each fly which emerged: the results show that the duration of the pupal stage is longer for male flies than for female flies. Data relating to the development of the male pupa, taken from Ludwig & Cable's paper, are given in Table 4. The lowest temperature at which the emergence of flies was observed was 15° C. Flies emerged from 96·4 % of the pupae which developed at this temperature. At 10° C. no flies emerged although partial development of the pupae goes on at this temperature; in a few instances the flies appeared to be fully formed within the pupal cases, but could not emerge. This may be due to incomplete development of the fly at this temperature; it may be due also to the low degree of activity of the fly at this temperature, which prevented its emergence from the pupal case. The actual developmental zero was not determined. Complete development of the pupa, to the emergence of the fly, can probably take place at temperatures somewhat lower than 15° C.

Table 4. *Showing time in days for the duration of the pupal stage of* D. melanogaster *(males) at the given constant temperatures*

Temp. °C. x	Flies emerged No.	%	Time in days y	Reciprocals $1/y$
15·0	40	96	14·15 ± 0·036	0·0706
20·0	92	97	6·78 ± 0·008	0·1474
22·5	63	99	5·27 ± 0·012	0·1897
25·0	118	98	4·26 ± 0·007	0·2347
26·0	35	100	4·00 ± 0·006	0·2500
27·0	108	98	3·78 ± 0·003	0·2645
27·5	110	100	3·65 ± 0·002	0·2739
28·00	71	96	3·56 ± 0·005	0·2809
28·5	47	93	3·45 ± 0·004	0·2898
29·0	104	100	3·40 ± 0·004	0·2941
29·5	105	100	3·35 ± 0·004	0·2985
30·0	66	96	3·35 ± 0·003	0·2985
31·0	21	93	3·35 ± 0·008	0·2985
32·0	24	78	3·50 ± 0·008	0·2857
33·0	17	39	3·63 ± 0·016	0·2757

The highest temperature at which complete development of the pupal stage to the emergence of flies was observed was 33° C. Flies emerged from only 38·7 % of the pupae developed at this temperature, which indicates that this high temperature is harmful to the developing pupa. At 34° C. no flies emerged, although, in a few instances, the fly appeared to be fully formed within the pupal case. The upper limit of temperature at which all development of the pupa is inhibited, was not determined.

The temperature at which development of the pupa proceeds at the fastest rate (peak temperature) was found to be 29·5° C. It was carefully determined by developing pupae in temperatures at half-degree intervals, over the range 27–30° C. (Table 4). The duration of the pupal stage at 29·5° C. was 3·35 days.

The temperature-velocity curve

The data given in Table 4 are plotted in Fig. 3. The closed circles represent the duration of the pupal stage in days (y) plotted against the appropriate temperatures (x). The open circles represent the average percentage development of the pupal stage, per day on the ordinate ($100/y$), plotted against the appropriate temperature on the abscissa (x). The observed values for $100/y$ at the temperatures 15–29·5° C. were fitted to a temperature-velocity curve having the formula

$$\frac{100}{y}=\frac{36\cdot76}{1+e^{4\cdot435754-0\cdot20036x}}.$$

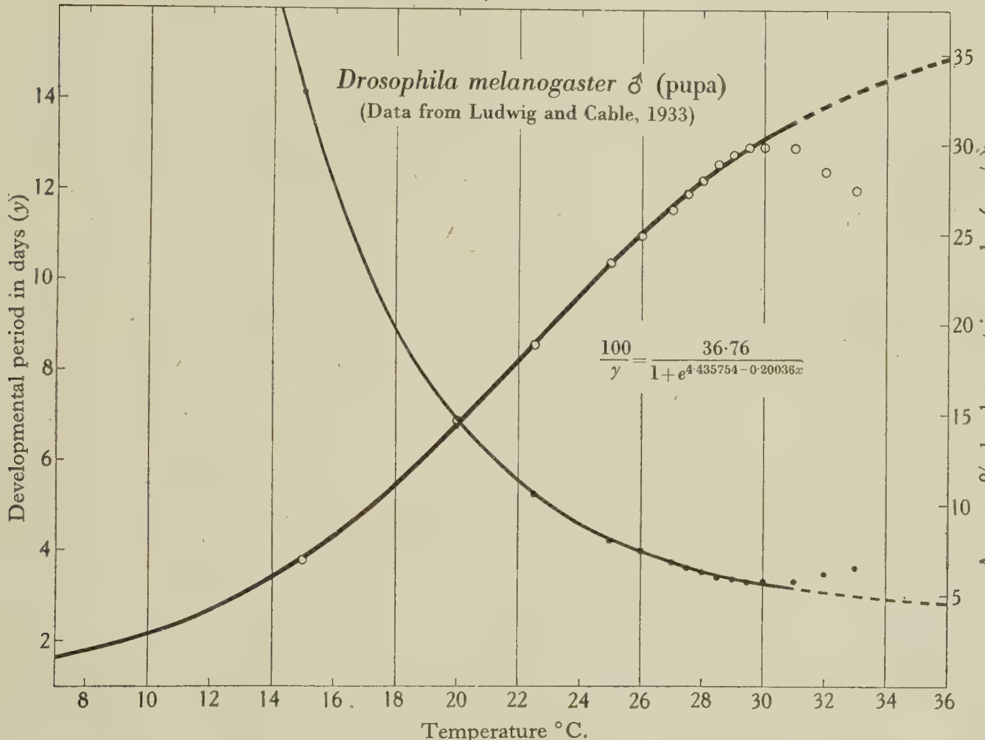

Fig. 3. Showing observed points on the temperature-time curve (closed circles) and temperature-velocity curve (open circles) for the pupal stage of *D. melanogaster*.

The curves shown in Fig. 3 were calculated from this formula. The value $K=36\cdot76$ was calculated from the following selected points on the projected curve:

x_1 at 15·0° C., $100/y=$ 7·06,
x_2 at 22·5° C., $100/y=18\cdot50$,
x_3 at 29·5° C., $100/y=29\cdot85$.

The observed values for $100/y$ at temperatures from 15 to 29·5° C. are a good fit to the calculated values. For each of these eleven values, the greatest deviation from the appropriate calculated point on the curve is 0·24 at 20° C., which is only 1·7 % of the calculated value. The root-mean-square deviation of the observed and calculated values is 0·1407: this deviation is only 1 % of the calculated value for $100/y$ at 20° C. The observed values for $100/y$ at temperatures above 29·5° C. fall short of the calculated values. The difference increases as the temperature rises (Fig. 3): at 30° C. the difference between the observed and calculated value is 2 % of the calculated value; at 31° C. it is 5·1 % of the calculated value. Above 31° C., there is a marked decrease in the number of flies which emerged in the experiments, which indicates the harmful effect of these high temperatures on the developing pupae.

The five additional examples given below illustrate further the suitability of the logistic curve for describing the trend in the speed of development of insects in relation to temperature. The essential data are given for each example so that the reader may work out the formula for the calculated curves.

4. SPEED OF DEVELOPMENT OF THE EGGS OF *MUSCA DOMESTICA*

Melvin (1934) carried out experiments on the incubation period of the eggs of *M. domestica*, and three species of Tachinidae, *Cochliomyia macellaria*, *Phormia regina* and *Lucilia sericata*, at constant temperatures (Table 5). The eggs were placed in humid

atmospheres at the temperatures stated, within 5 min. of being laid: the temperatures were constant to one-tenth of a degree. During the periods the eggs were hatching, observations were made, at 10 min. intervals, and the number of larvae which had hatched out was recorded. The incubation periods

Table 5. *Showing incubation period in hours for the eggs of* A, Musca domestica; B, Cochliomyia macellaria; C, Phormia regina; D, Lucilia sericata, *at the given constant temperatures. Data from Melvin* (1934)

Temp. °C.	A	B	C	D
15·0	51·45	—	51·97	42·37
17·8	33·28	32·98	34·42	29·42
20·6	23·08	22·04	24·14	20·89
23·3	17·16	16·02	18·10	15·78
26·1	13·50	12·08	14·32	12·63
28·9	10·65	9·66	11·42	10·25
31·7	9·00	8·16	9·51	8·82
34·4	8·14	7·26	8·55	8·10
37·2	7·63	6·65	8·13	8·09
40·0	8·05	6·73	8·70	—

about 36° C. The observed values for $100/y$ at 15–37·2° C., computed from the data given in Table 5, were fitted to a temperature-velocity curve having the formula

$$\frac{100}{y} = \frac{15{\cdot}17}{1 + e^{4{\cdot}480468 - 0{\cdot}172223x}}.$$

The curve shown in Fig. 4 was calculated from this formula. The value $K = 15{\cdot}17$ was calculated from the following selected points on the projected curve:

x_1 at 15·0° C., $100/y = 1{\cdot}944$,
x_2 at 24·7° C., $100/y = 6{\cdot}700$,
x_3 at 34·4° C., $100/y = 12{\cdot}285$.

The nine observed values for $100/y$ at 15–37·2° C. are a remarkably good fit to the calculated curve. For all these values, the greatest deviation from the appropriate point on the calculated curve is 0·233 at 26·1° C., the deviation being 3 % of the calculated value: the root-mean-square deviation for the observed and calculated values is 0·1091, which is only 1·4 % of the calculated value at 26·1° C.

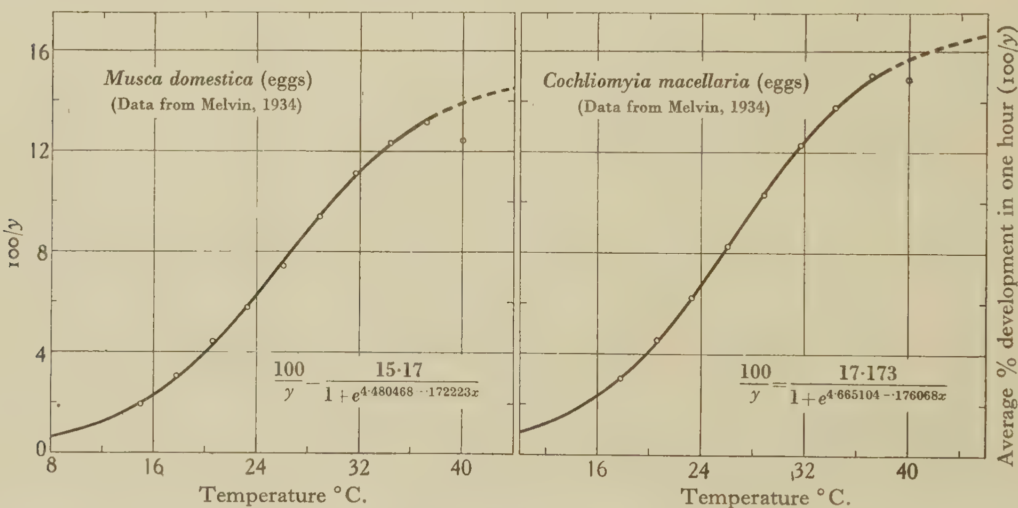

Fig. 4. Showing the observed points on the calculated temperature-velocity curve for *M. domestica* and *C. macellaria*.

in hours given in Table 5 represent the weighted means of from 3000 to 5000 eggs which hatched at each temperature. The trend of the speed of development of the eggs of *Musca domestica* in relation to temperature is shown in Fig. 4. The observed points represent the average percentage development of the eggs per hour, on the ordinate ($100/y$), plotted against the appropriate temperature on the abscissa (x). The upper and lower limit of temperature, at which the eggs will develop completely to hatching, was not determined. Some eggs hatched at 41·6° C., but none hatched at 42·8° C. The peak temperature was not determined: it may be placed tentatively

5. SPEED OF DEVELOPMENT OF THE EGGS OF *COCHLIOMYIA MACELLARIA*

The trend of the speed of development of the eggs of *C. macellaria* in relation to temperature is illustrated in Fig. 4. The points represent the reciprocal values × 100 ($100/y$) for the incubation period of the eggs (Table 5), plotted against temperature (x). At 15° C. only about 10 % of the eggs hatched: some eggs hatched at 41·6° C., but none hatched at 42·8° C. The peak temperature was not determined: it may be placed tentatively about 36° C. The observed values for $100/y$ at 17·8–

34·4° C., calculated from Table 5, were fitted to a curve having the formula

$$\frac{100}{y}=\frac{17\cdot173}{1+e^{4\cdot665104-0\cdot176068x}}.$$

The temperature-velocity curve shown in Fig. 4 was calculated from this formula. The value $K=17\cdot173$ was calculated from the following selected points on the projected curve:

x_1 at 17·8° C., $100/y=3\cdot03$,
x_2 at 26·1° C., $100/y=8\cdot28$,
x_3 at 34·4° C., $100/y=13\cdot77$.

The seven observed values for $100/y$ from 17·8–34·4° C. are a good fit to the calculated curve. The greatest deviation of any of the values from the appropriate point on the calculated curve is 0·046 at 20·6° C.: this is only 1 % of the calculated value. The root-mean-square deviation for the seven observed and calculated values is 0·0238, which is only 0·53 % of the calculated value at 20·6° C.

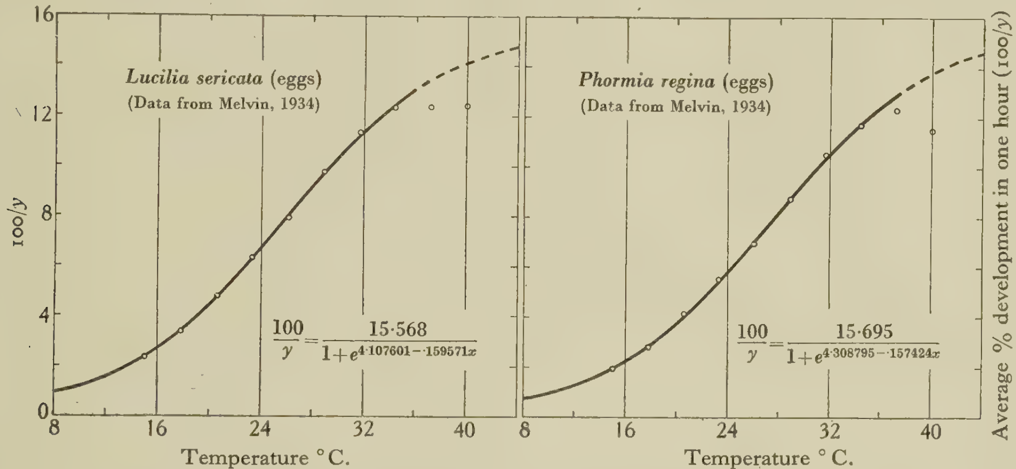

Fig. 5. Showing observed points on the calculated temperature-velocity curve for development of the eggs of *Phormia regina* and *Lucilia sericata*.

6. SPEED OF DEVELOPMENT OF THE EGGS OF *PHORMIA REGINA*

The values for $100/y$ for the incubation period of the eggs of *Phormia regina* (Table 5) are plotted against temperature in Fig. 5. The upper and lower temperature limit for development was not determined: some eggs hatched at 41·6° C., but none hatched at 42·8° C. The peak temperature lies between 34·4 and 37·2° C., and may be placed tentatively at 36° C.

The observed values for $100/y$ at 15·0–34·4° C., calculated from the data given in Table 5, were fitted to a temperature-velocity curve having the formula

$$\frac{100}{y}=\frac{15\cdot695}{1+e^{4\cdot308795-0\cdot157424x}}.$$

The curve presented in Fig. 5 was calculated from this formula. The value $K=15\cdot695$ was calculated from the following selected points on the projected curve:

x_1 at 17·8° C., $100/y=2\cdot82$,
x_2 at 26·1° C., $100/y=6\cdot98$,
x_3 at 34·4° C., $100/y=11\cdot70$.

The eight observed values for $100/y$ at 15–34·4° C. are a good fit to the curve. The greatest deviation of any of these values from the appropriate point on the calculated curve is 0·122 at 20·6° C.; this is 3 % of the calculated value at this temperature. The root-mean-square deviation for all the eight values is 0·08423, which is only 2·1 % of the calculated value at 20·6° C. The observed values depart from the calculated curve, at temperatures above about 36° C.: the observed value of $100/y$ at 37·2° C. is 0·641, which is almost 5 % of the calculated value.

7. SPEED OF DEVELOPMENT OF THE EGGS OF *LUCILIA SERICATA*

The values for $100/y$ for the incubation period of the eggs of *L. sericata* given in Table 5 are plotted against temperature in Fig. 5. The upper and lower limits of temperature, at which development ceases, were not determined: some eggs hatched at 40° C., but no eggs hatched at 41·6° C. The peak temperature lies between 34·4 and 37·2° C. and may be placed tentatively at 36° C.

The values observed for $100/y$ at 15–34·4° C. were fitted to a curve having the formula

$$\frac{100}{y}=\frac{15\cdot568}{1+e^{4\cdot107601-0\cdot159571x}}.$$

The temperature-velocity curve presented in Fig. 5 was calculated from this formula. The value

$K = 15{\cdot}568$ was calculated from the following selected points on the projected curve;

$$x_1 \text{ at } 17{\cdot}8^\circ \text{ C.,} \quad 100/y = 3{\cdot}40,$$
$$x_2 \text{ at } 26{\cdot}1^\circ \text{ C.,} \quad 100/y = 7{\cdot}92,$$
$$x_3 \text{ at } 34{\cdot}4^\circ \text{ C.,} \quad 100/y = 12{\cdot}35.$$

The eight observed values for $100/y$ at temperatures 15–34·4° C. are a good fit to the calculated curve. The greatest deviation of any of these values, from the appropriate calculated point on the curve, is 0·109 at 31·7° C.: this is barely 1 % of the calculated value at this temperature. The root-mean-square deviation for all the eight points is 0·06704, which is only 0·51 % of the calculated value at 31·7° C.

8. SPEED OF DEVELOPMENT OF THE EGGS OF *EPHESTIA KÜHNIELLA*

Voûte (1936) did experiments on the rate of development of the eggs of the moth *E. kühniella* at constant temperatures: the relevant data are given in Table 6. The eggs were laid at the temperatures in which they were subsequently incubated. At 13° C. the moths laid very few eggs, and no eggs were laid at lower temperatures. The moths also laid very few eggs at 33° C., and no eggs were laid at higher temperatures. Although the lowest temperature at which records are given for hatching of the eggs is 13° C., complete embryonic development to hatching occurred, in a few instances, at 10° C.; even at 8° C. some development of the embryo was observed, but complete development to hatching cannot take place at this low temperature. The upper limit of temperature at which development ceases was not determined: the moths soon died at 33° C. and the mortality of the eggs was high (Table 6). The shortest observed time for complete development of the eggs to hatching, was 3·1 days at 32° C. It should be noted that Janisch (1925) and Janisch & Maercks (1933) placed the shortest time for the development of the eggs of *E. kühniella* as 3·75 days at 29·6° C., but this value is based on one observation only. Janisch arranged for the moths in his experiments to lay their eggs at 18° C.: the eggs were then transferred to selected temperatures for incubation. The difference in the incubation periods, obtained at various temperatures, by Janisch and Voûte, may be due, to some extent, to the different temperatures at which the moths laid their eggs. However, Voûte appears to have maintained better controlled temperature conditions in his experiments.

Table 6. *Showing incubation period for the eggs of* E. kühniella *at the given constant temperatures: data from Voûte* (1936)

Temp. °C. x	Time in days y	Mortality of eggs %	Reciprocals
13·0	21·0 ± 0·9	14	0·0476
15·5	14·0 ± 0·1	17	0·0714
16·0	13·3 ± 0·3	7	0·0752
17·5	10·0	9	0·100
21·0	6·1 ± 0·2	15	0·1639
22·25	5·4 ± 0·6	16	0·1852
25·5	4·1 ± 0·3	11	0·2439
26·0	4·0	17	0·250
27·0	3·8 ± 0·5	29	0·2632
29·0	3·5 ± 0·4	33	0·2857
30·0	3·3 ± 0·3	12	0·3030
32·0	3·1 ± 0·2	16	0·3226
33·0	3·7 ± 0·5	84	0·2703

The observed data given in Table 6 are plotted in Fig. 6. The observed values for $100/y$ at 13 to 32° C., were fitted to a curve having the formula

$$\frac{100}{y} = \frac{36{\cdot}35}{1 + e^{4{\cdot}595759 - 0{\cdot}206667x}}.$$

The temperature-velocity curve in Fig. 6 was calculated from this formula. The value $K = 36{\cdot}35$ was calculated from the following selected points on the projected curve:

$$x_1 \text{ at } 15{\cdot}75, \quad 100/y = 7{\cdot}3,$$
$$x_2 \text{ at } 23{\cdot}87, \quad 100/y = 21{\cdot}3,$$
$$x_3 \text{ at } 32{\cdot}00, \quad 100/y = 32{\cdot}3.$$

The 12 observed values for $100/y$ from 13 to 32° C. are a good fit to the calculated curve. The greatest deviation from the curve, of any of these values, is 0·333 at 16° C.: this is 4·2 % of the calculated value: the root-mean-square deviation for the observed and calculated values is 0·2887 which is 3·7 % of the calculated value at 16° C.

9. DISCUSSION

The logistic curve described in this paper gives an empirical representation of the trend in the rate of development of insects at constant temperatures, throughout the greater part of the range of temperature suitable for development. The mathematical formula of the curve implies that, under the given conditions, the particular species of insect has an inherent power of attaining the average speed of development, represented by the value of the parameter K. In the case of the embryo of *Drosophila melanogaster* (Fig. 1), this value is 7·1 % per hour of the total development of the embryo. The temperature at which this rate of development would be achieved, based on the calculated curve, would be 42° C. The embryo cannot attain this rate of growth because its development is inhibited about 34° C. The parameter K may be looked upon as a theoretical, biological constant. Its value may be different for different species of insects and for different stages of the life cycle of the same species: it may differ also for different strains of the same species. The value remains constant for a particular set of conditions in the external environment; any change in

this environment which brings about a change in the rate of development, such as the degree of moisture, may result in a change in the value of K.

The trend of the velocity curve from the hatching zero (14·5° C.) to the peak temperature (about 29·5° C.) for *D. melanogaster* (Fig. 1) shows that the relative rate of acceleration of development gradually increases with rise in temperature until the inflexion of the curve (21·48° C.) is reached. At temperatures above the inflexion, the relative rate of acceleration decreases with rise in temperature until the peak temperature is reached. This is the temperature at which the development of the embryo proceeds at the fastest average rate. At temperatures above the peak the relative rate of acceleration of development declines rapidly: at 34° C. the embryo is unable to develop to completion.

We may consider that two sets of forces in the experiments determine the trend of the observed points: (1) the inherent potentiality of the embryo, which is striving to attain the theoretical speed of development represented by $K=7{\cdot}1$ % per hour: (2) the forces associated with heat, which increase or retard the speed of development. The relative increase in the rate of development of the embryo, at temperatures below the inflexion of the curve, is not maintained at temperatures above the inflexion, because of the retarding forces which slow down the rate of development as the temperature is raised. Above the 'peak', these effects are intensified, and the observed values for rate of development fall significantly below the calculated values. This indicates that the effects are different in kind or intensity: they do not conform to the same rules as for the lower temperatures, otherwise the observed values for temperatures above the peak would follow the computed curve.

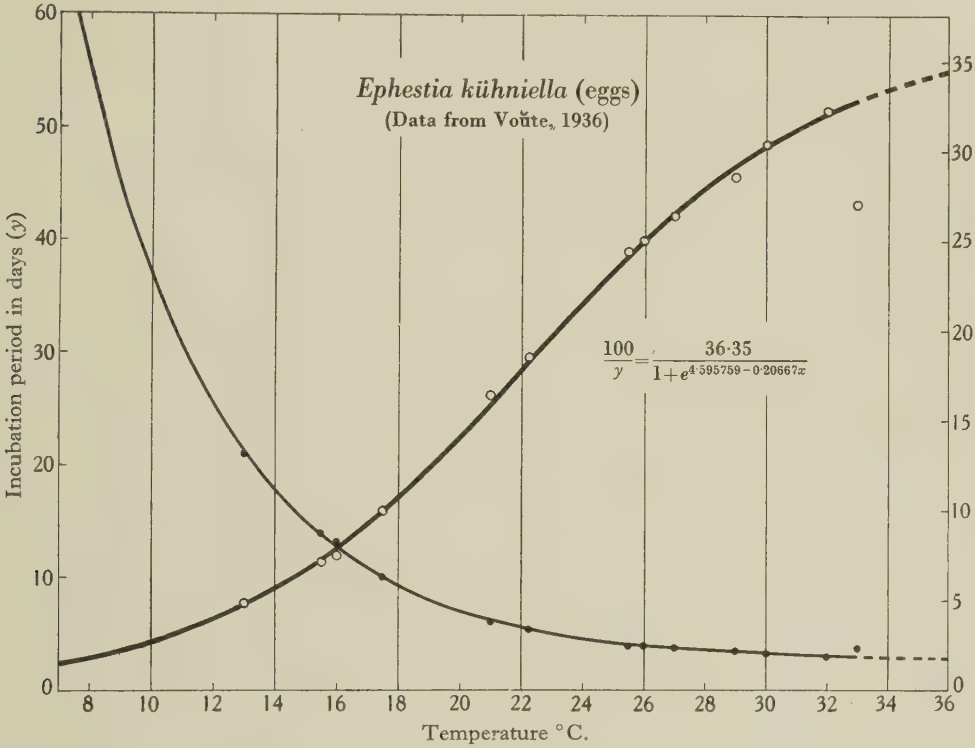

Fig. 6. Showing observed points on the temperature-velocity curve (open circles) and temperature-time curve (closed circles) for the development of the eggs of *E. kühniella* at constant temperatures. Data from Voûte, 1936.

Effect of higher temperatures

With experiments on temperature and development it is always found that, at temperatures above the peak, there is a marked increase in the number of individuals which die without completing their development. This rapid increase in mortality indicates that the insects experience harmful effects at these 'higher' temperatures. The relation of these things to the physiology of the animals is not yet understood: they may be associated with the diffusion of oxygen and carbon dioxide in the tissues, or the accumulation of waste products of metabolism. Buddenbock & Rohr (1922) showed that the efficiency of respiration of pupae of *Calliphora vomitoria*, as determined by the intake of oxygen,

changes about 25° C., resulting in a fall in the amount of oxygen consumed. Gunn (1933) found that the rate of water loss with *Blatta orientalis* is much greater above 30° C., owing to a change in the mechanism of respiration from regulation by diffusion to regulation by ventilation, about this temperature. Fraenkel & Herford (1940), from observations on the larvae of *Calliphora erythrocephala*, concluded that the cause of death of these larvae at 40° C. is related to the accumulation of acid waste products of metabolism.

The observations of these investigators support the view that the 'higher' temperatures have a harmful influence on the development of insects. The degree of harm is greater with the more advanced stages of the life cycle of the insect: in an early stage partial development may go on for a time, at temperatures which are too high to allow of the particular stage developing to completion. These features have been referred to already in the case of the embryo and pupa of *Drosophila melanogaster*. Meyer (1935) considers that the harmful effects of 'higher' temperatures may be greater on the more advanced stages of the embryo of the frog *Rana pipiens*, because the heat may have a different effect on different organs: Meyer's observations indicate that the rate of development of one or more structures in the embryo may fail to keep pace with the development of the remaining organs. This differential effect on the various organs results in the production of unhealthy or abnormal individuals.

Melvin (1928) stated that metabolic activity of the embryo of the silkworm moth *Tropaea luna* L. is relatively low during the first day of its development; it takes in very little oxygen. During the last day of its development metabolic activity is high, and the embryo takes in a relatively large amount of oxygen.

These aspects of the physiology of insects illustrate how, in an early stage of the growth of an insect, development of the early stage may go on to completion over a wider range of temperature, than is the case with a more advanced stage of the development of the insect. The 'optimum' temperature for development is now often defined as that temperature at which the largest number of individuals are able to complete their development and become healthy insects. It may include a range of several degrees: it is not necessarily the temperature at which development proceeds at the fastest rate.

The Van t'Hoff-Arrhenius equations

The Van t'Hoff and Arrhenius equations were developed to illustrate the relationship between temperature and the acceleration of chemical and physical reactions. The Van t'Hoff equation may be written

$$Q_{10} = \left(\frac{y_1}{y_2}\right)^{10/(x_1-x_2)},$$

where y represents velocity for development at the given temperature x in degrees centigrade. When applied to the effect of temperature on the rate of growth of insects, the Van t'Hoff formula implies that the ratio of increase in the rate of development produced by a given difference in temperature (Q_{10}) remains constant. The Arrhenius equation, which represents a further development of the van t'Hoff formula, may be written

$$\frac{y_2}{y_1} = e^{\frac{1}{2}\mu(1/x_1 - 1/x_2)},$$

when y represents velocity for development at the given temperature x, temperature being in degrees absolute. This formula relates the value of the 'temperature characteristic' (μ) to the amount of work being done by the developing insect at different temperatures. It has been shown that these equations are inadequate for relating temperature to the speed of development in poikilothermic animals. Values for the Q_{10} ratio and the temperature coefficient (μ) remain constant only for a very restricted part of the range of temperature at which development goes on. Ryan (1941) found with the development of the embryo of the frog *Rana pipiens* that the Van t'Hoff equation may be applied to the observed data in the upper part of the temperature range in which development goes on—that is up to the 'peak' temperature: the Arrhenius equation may be applied to the observed data in the lower portion of the temperature range.

The application of the Arrhenius equation to temperature-development data is well illustrated by the work of Bliss (1926) on the prepupal stage of *Drosophila melanogaster*. Complete development of this stage of the insect was obtained at temperatures ranging from 12 to 33° C. The calculated values for μ were as follows:

Between 12 and 16° C.	33,210
Between 16 and 25° C.	16,850
Between 25 and 30° C.	7,100

At temperatures above 30° C. the temperature-time data could not be fitted to the equation. The occurrence of the three different value for μ, each value having its own restricted range of temperature, has been interpreted as revealing that the velocity of the changes in the physiology of the insect, associated with its development, are determined by a limiting 'master reaction': in this instance three master reactions appeared between 12 and 30° C. With this kind of reasoning, however, it would be possible to subdivide the complete range of temperature, suitable for the development of a given insect, into any convenient number of subdivisions, each division having its own value for μ.

The formula for temperature summation

The theory of summation of temperatures which is widely used by entomologists to relate tempera-

ture and development in insects implies that the temperature-time curve is a hyperbola and its reciprocal a straight line. The equation may be written:

$$y(x-a) = \text{thermal constant},$$

where y represents time required for development at the given temperature x in degrees centigrade; a is the theoretical zero temperature for development. It is generally understood that the observed reciprocal values fall on the straight line only in the median portion of the total range of temperature at which development goes on. Since the temperature-time curve has an exponential form, the reciprocal curve being S-shaped, it is evident that the temperature-summation theory is an unsatisfactory representation of the facts and its use should be discontinued.

The formula of Bělehrádek

The equation of Bělehrádek (1926, 1935) may be written

$$y = \frac{a}{xb} \quad \text{or} \quad y = \frac{a}{(x-c)^b},$$

where y represents the time required for development at temperature x in degrees centigrade, a, b and c are constants: the constant b is intended to represent a temperature coefficient. This equation implies that, when log values for the time required for the development of a given stage in the life cycle of an insect, at different tenperatures, are plotted against log values for the appropriate temperature, the points lie on a straight line. The data for *D. melanogaster* have been plotted in this way (Fig. 2B). The fit of the data to the straight line holds over a wider range of temperature than when the reciprocal values for time are plotted against the appropriate temperatures: the fit does not extend over such a wide range of temperature as that obtained by the straight line representation of the logistic curve (Fig. 2A).

The catenary curve of Janisch

Janisch (1925) brought forward the view that the time-temperature relationship for insect development can be expressed by a catenary curve,

$$y = \frac{m}{2}(a^x + a^{-x}),$$

where y represents the time required for development at the given temperature x in degrees centigrade: m is the time for development at the optimum temperature, a is a constant. This author maintained that the curve shows the trend of the observed data throughout the whole range of temperature at which the development of a given stage can go on. This view was developed further in later papers (see Uvarov, 1931). The catenary curve is a general, empirical curve. The original data used by Janisch to illustrate its application to the development of insects, were obtained by experiments on embryonic development in the Mediterranean flour moth, *Ephestia kühniella*. Data relating the embryonic development of the cattle tick, *Margaropus annulatus*, were also used. The data are relatively poor compared with those obtained by later investigators, which is due, to some extent, to improved methods employed in the experiments by later workers. Janisch does not critically test the 'goodness of fit' of the observed data to the calculated catenary curve. Data for embryonic development in *Ephestia kühniella* obtained by Voûte differ considerably from those obtained by Janisch. Voûte considers that the observed points at temperatures above the 'peak', do not fit a catenary curve (Fig. 6). The writer (1942) considers that the use of the catenary curve, as applied by Janisch, is not justified. Data for development at temperatures above the 'peak' are unreliable because of harmful effects at these temperatures: these harmful effects are intensified as the time of exposure is increased.

The logistic curve

The logistic curve here described is also a general empirical curve. It represents the trend of the reciprocal values for observed temperature-time data for the development of insects throughout 85–90 % of the range of temperature at which development can go on. As stated by Needham (1931, 1: 533) there are advantages in using empirical curves for describing the relation of temperature to rate of development, although they have not got the same value as equations having a definite physical meaning such as the Arrhenius equation. It is seen in Figs. 1 and 3 that the observed data for rate of development at temperatures above the 'peak', may be represented by a curve of the form

$$\frac{100}{y} = \frac{K}{1+e^{a+bx}}.$$

The calculated constants for this curve would have little value because observed data can be obtained only for a very small part of the projected curve.

10. SUMMARY

1. The following equation has been used to show the relationship between temperature and the time required for development in insects and other poikilothermic animals:

$$\frac{1}{y} = \frac{K}{1+e^{a-bx}}.$$

$1/y$ represents the reciprocal value of the time required for a given stage in the life cycle of an insect, to develop at a given temperature x; K, a and b are constants. The calculated values for $1/y$,

when plotted against appropriate values for temperature (x) describe an S-shaped velocity curve. The equation is a form of the logistic curve in which the value for K represents the upper asymptote of the curve.

2. The methods used in calculating the curve are described in detail from data relating the development of the egg and pupal stage of *Drosophila melanogaster* at constant temperatures. The data are taken from papers by Ludwig & Cable (1933), and Powsner (1935).

3. Data on the rate of embryonic development in four species of Diptera, given by Melvin (1934), and for *Ephestia kühniella*, given by Voûte (1936), have been fitted to this form of curve. The curve faithfully represents the trend of the speed of development of insects, for 85–90 % of the complete range of temperature at which development can go on. The 'peak' temperature is defined as the temperature at which the given stage of the animal develops at the fastest average rate. At temperatures above the 'peak', the observed values for rate of development are significantly less than the calculated values: the range of these temperatures represents 10–15 % of the total range of temperature at which development can go on.

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REFERENCES

Bělehrádek, J. (1926). C.R. Soc. Biol., Paris, 95: 1449–52.
Bělehrádek, J. (1935). 'Temperature and living matter.' Borntraeger, Berlin.
Bliss, C. J. (1926). J. Gen. Physiol. 9: 467–95.
Brindley, T. A. (1930). Ann. Ent. Soc. Amer. 23: 741–57.
Buddenbrock, W. von & Rohr, G. von (1922). Pflüg. Arch. Ges. Physiol. 194: 468–72.
Davidson, J. (1938). Trans. Roy. Soc. S. Aust. 62 (1): 141–8.
Davidson, J. (1942). Aust. J. Exp. Biol. Med. Sci. 20: 233–9.
Fraenkel, G. S. & Herford, G. V. B. (1940). J. Exp. Biol. 17: 386–95.
Gause, G. F. & Alpatov, W. W. (1931). Biol. Zbl. 51: 1–14.
Gunn, D. L. (1933). J. Exp. Biol. 10: 274–85.
Janisch, E. (1925). Pflüg. Arch. Ges. Physiol. 209: 414–36.
Janisch, E. & Maercks, H. (1933). Arb. Biol. Abt. (Anst.—Reichsanst.), Berl. 20: 259–68.
Lotka, A. J. (1925). 'Elements of physical biology,' Ch. 8. Baltimore.
Ludwig, D. (1932). Physiol. Zoöl. 5: 431–47.
Ludwig, D. & Cable, R. M. (1933). Physiol. Zoöl. 6: 493–508.
Melvin, R. (1928). Biol. Bull. Woods Hole, 55: 135–42.
Melvin, R. (1934). Ann. Ent. Soc. Amer. 27: 406–10.
Atlas, Meyer (1935). Physiol. Zoöl. 8: 290–310.
Needham, J. (1931). 'Chemical embryology', vol. 1. Cambridge.
Pearl, R. (1930). 'Medical biometry and statistics', 2nd. ed., Ch. 17. Philadelphia.
Pearl, R. & Reed, L. J. (1920). Proc. Nat. Acad. Sci., Wash. 6: 275–88.
Powsner, L. (1935). Physiol. Zoöl. 8: 474–520.
Ryan, F. J. (1941). J. Exp. Zool. 88: 25–54.
Uvarov, B. P. (1931). Trans. R. Ent. Soc. Lond. 79: 1–247.
Voûte, A. D. (1936). Z. Angew. Entom. 22: 1–25.

STUDIES OF THE BEHAVIOUR OF THE TSETSE-FLY (*GLOSSINA PALLIDIPES*) IN THE FIELD: THE ATTRACTIVENESS OF VARIOUS BAITS

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(With 1 Figure in the Text)

1. INTRODUCTION

(*a*) *Object*

The object of the investigation described below was to determine the relative efficacy of various animals in attracting *Glossina pallidipes* Aust.

Previous work on this subject, but without close comparisons, has been done by Swynnerton (1921), Jack (1941), Harris (1930), Lloyd (1935), and Potts (unpublished).

(*b*) *Site*

These observations were carried out inside a thorn and manyara (*Euphorbia tirucalli*) thicket barrier (Fig. 1), which borders one side of an experimental area of *Acacia-Commiphora* bush (Swynnerton, 1936). The thorn thicket barrier has been produced from an old clearing, in which the large trees had been felled, by exclusion of grass fires for 10 years. Thickening was aided by the planting of a few small patches of *Euphorbia tirucalli* in the thin areas. *Dichrostachys glomerata* has become particularly thick in patches under fire exclusion. The thorn thicket barrier is 300 yd. wide and 1200 yd. in length. Cutting its end is a strip of natural riverine thicket bordering the seasonal manyara stream. The riverine strip is 150 yd. wide, and on its right bank begins the manyara thicket barrier. The latter is almost entirely artificial, being composed of *Euphorbia tirucalli* and a few small patches of natural thicket that were left at the time of planting. The manyara barrier is 100 yd. wide and 2660* yd. in length; it ends against the natural thickets of the Ninghwa river. The thorn thicket is deciduous and averages 8–10 ft. in height; the riverine thicket is partly evergreen and partly deciduous, the undergrowth being about 6 ft. high and overshadowed by large acacias and figs which rise to a height of 30 or 40 ft. The manyara barrier is evergreen and almost impenetrable to man without the aid of an axe. Its height varies from 10 to 15 ft. according to the locality; the upper branches are so much interlaced as to form a thick canopy excluding most of the sunlight.

* Swynnerton (1936), pp. 316–18 gives the manyara barrier as 1·74 miles (3062 yd.); it appears that this measurement must have included a section south of the Ninghwa river not used in the rounds.

(*c*) *Methods*

A catching path was cut down the middle of the thicket and manyara barriers. This path is divided into three stages, the first being in the thorn thicket, the second in the riverine and manyara, and the third solely in the manyara thicket. These stages are approximately equal in length, each being just over 1250 yd. They did not run the whole length of the barrier. The observations were carried out between January 1939 and July 1940, with a variety of domestic and wild animals as baits. The animals were ox, dog, domestic pig, sheep, goat, baboon, porcupine, lion, serval cat, jackal, kudu, reedbuck and Thomson's gazelle; with these a variety of attractant T-shaped screens were compared.

Two types of catches were employed; the moving catch where the bait animal is led along the path stopping at intervals to enable the catchers to take the flies; and stationary catches where the bait animal is tethered at some set point along the path, and the flies are caught as they appear and are recorded against the time of day.

(*d*) *Scope of investigation*

It was not practicable to contrast several individuals of any species with several of all the others, though experiments to test individual differences between oxen have been initiated and are continuing. It is therefore theoretically conceivable that the differences found are individual and not specific; but the differences observed are considerable, and it seems far more likely that they are very largely specific. The significant differences obtained mean that, if the observations were multiplied to infinity, those animals concerned would not be likely to change their order of attractiveness; though of course all the others tested would then also become significantly different from each other.

2. RESULTS FROM THE MOVING CATCHES

It was not possible to make direct comparative catches on the moving rounds, since the leading animal would attract all the flies and the following animal fail to obtain any. So the moving rounds were done twice daily, once in the morning and once

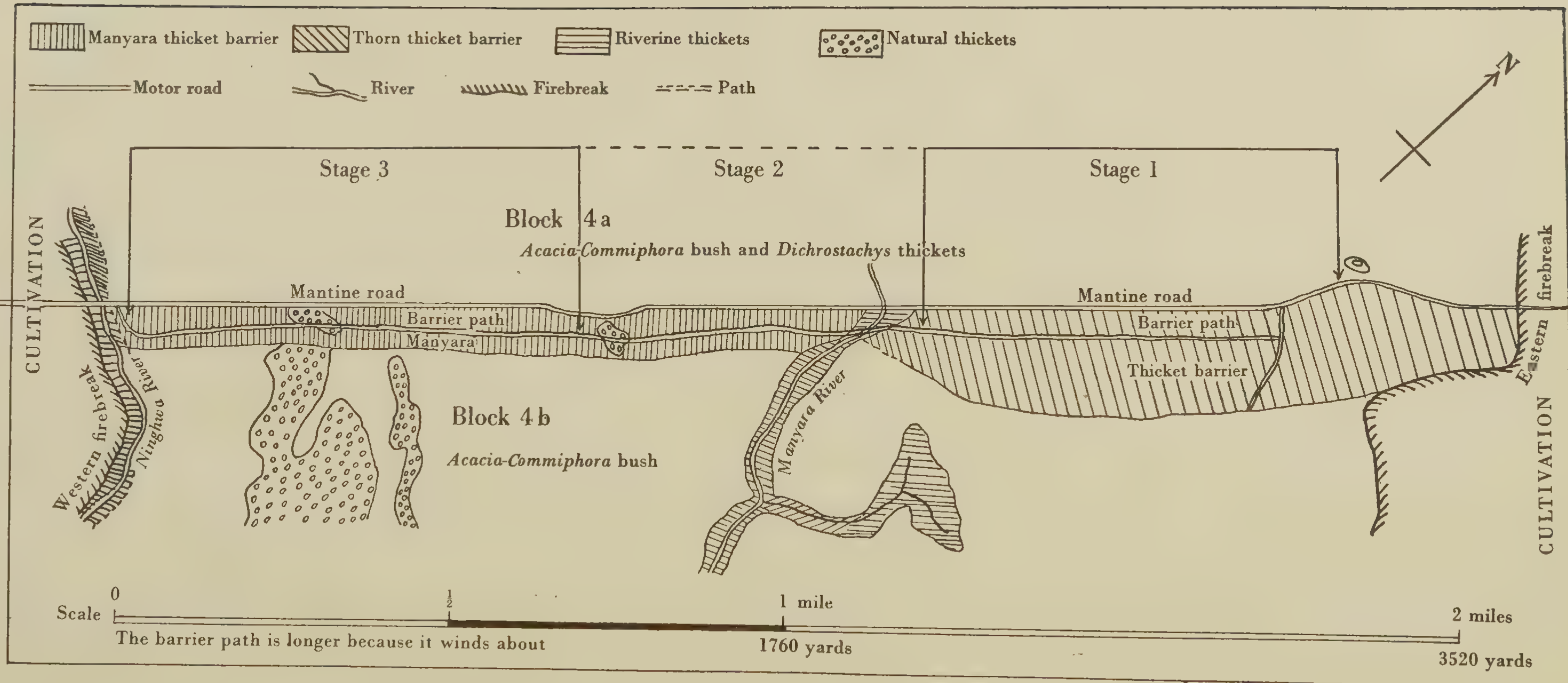

Fig. 1. Diagram of the area.

in the afternoon, and the bait animals were used in rotation on the morning and afternoon rounds. The following rotation of baits was used: screen, man only, ox, sheep, goat, dog, baboon, and domestic pig. The attractant screen was of the T-hand-catching type covered with black material (Swynnerton, 1936). A pair of lion cubs, a serval cat and a jackal were used for short periods in rotation with the other baits, but not throughout the whole experiment. The following table gives the results obtained. The catches-plus-one have been converted into logarithms, so that when graphed as frequencies they have approximately normal distribution curves (Williams, 1937).

Table 1 gives the arithmetic and geometric mean catches of males and females on the various baits. The geometric mean has been obtained by taking the arithmetic mean of the sum of all the logarithms of each catch-plus-one, and then reconverting back into a number and subtracting one. Two oxen, numbered A and B, both about the same size and black all over, were used. The dog used was a large cross between a wolfhound and local mongrel, and completely white.

Table 1*a* compares the catches of males on the various baits and shows which are significantly different (P taken as, or less than, 0·05).

Table 1*b* compares the catches of females from those baits that attracted them; only one female was taken on goat and none on baboon and serval cat.

Table 1*c* compares the total (male and female) catches from each of the baits, and includes those animals from which only male flies were taken. This shows several more pairs of observations that are significantly different from each other than when either male or female catches were considered separately.

The original data from these observations are set out in Appendix 1.

Two young lions, 6 months old, were used on ten occasions, also two adult jackals; however, no *G. pallidipes* were taken on these animals.

3. ATTRACTANT SCREENS COMPARED

Comparative catches were carried out in the same area, but over a longer round, with three different screens, from January to October 1939. There were two large screens, with a total surface area of 2 sq.m. one of which was 'scented'. The third screen was smaller with a total surface of 1·5 sq.m. Inside the scented screen were sacks which had been used to lay the bush-pigs upon when feeding tsetses on them. The sacks smelt very strongly of pig, and the screen itself was kept hung over the pigs' pen in the zoo when not in use (Table 2).

Although the 'scented' large screen caught more flies per round than the unscented large screen, there is no significant difference between the two.* However, the small screen took significantly less than either of the other two. These figures have been tested in the same manner as the observations described above. The large unscented screen appears to take more flies per square metre than the small one, the proportions being (from arithmetic means) 1·68 to 1·00.

The proportion of females taken on these three screens varies from 14 to 16 % of the total catch (Appendix 1).

4. RESULTS FROM THE STATIONARY CATCHES

(*a*) *Catches in rotation*

The stationary catches were carried out in the manyara thicket a few hundred yards away from its junction with the riverine thicket at the Manyara river. The animal was tethered and one catcher watched each side of the animal. The flies were recorded against the time of day in quarter-hour intervals. The numbers caught each hour are taken as a unit observation (Table 3).

The geometric mean catches of males on the above baits are all significantly different from each other except those on sheep and goat, and goat and baboon. The mean catches of females show that those on ox and domestic pig are significantly different from each other and from all the other baits used, but catches on sheep, goat and baboon are not significantly different from each other. Total males and females give the same results as for the males alone.

Besides those baits listed above, Thomson's gazelle was used for a total of 12 hr. during January 1939 only and took one male. A reedbuck was used for 7 hr. during September 1939 and one male was taken. A serval cat was used for a total of 35 hr. from January to March 1939 and failed to attract any flies as did the two lion cubs that were used for 31 hr. each during May to July 1939.

(*b*) *Simultaneous catches*

Some direct comparisons from simultaneous stationary catches on various baits were made in the same locality during March to July 1940. The two animals were tethered 50 yd. apart in the manyara thicket and completely hidden from each other; their positions were interchanged hourly.

The order of preference for attractiveness of these baits is the same as given in Table 3, and the same as obtained for the moving catches, with the exception of domestic pig. The pig was not a good subject

* Recent investigations with alcohol and ether extracts from the body surface of living bush-pig, ox, and sheep have shown significantly increased catches over those from unscented screens. F.L.V.

Table 1. *Mean catches of male and female* G. pallidipes *on various baits*

Baits ...	Ox A	Ox B	Screen	Man	Sheep	Goat	Baboon	Domestic pig	Dog	Serval cat
No. of obs. ...	24	25	92	43	43	45	40	44	12	9
Males:										
Arithmetic mean	4·08	3·36	2·60	2·58	1·54	1·36	1·95	1·75	3·17	0·55
Geometric mean	2·53	2·31	1·42	1·23	0·92	0·80	0·86	0·97	2·64	0·42
Females:										
Arithmetic mean	2·46	1·08	0·43	0·05	0·09	0·02	0·00	0·16	0·00	0·00
Geometric mean	1·14	0·78	0·25	0·03	0·07	—	—	0·10	—	—

Table 1*a*.

Male *G. pallidipes* caught off

	Dog	Ox B	Screen	Man	Domestic pig	Sheep	Baboon	Goat	Serval cat
Ox A	—	—	$P=0·09$	$P=0·07$	+	+	+	+	+
Dog		—	+	+	+	+	+	+	+
Ox B			$P=0·09$	$P=0·07$	+	+	+	+	+
Screen				—	—	+	$P=0·015$	+	+
Man					—	—	—	—	+
Pig						—	—	—	$P=0·06$
Sheep							—	—	$P=0·1$
Baboon								—	—
Goat									$P=0·2$

+ denotes $P=0·05$ or less. — denotes not significant.

Table 1*b*

Female *G. pallidipes* caught off

	Ox B	Screen	Man	Sheep	Domestic pig
Ox A	—	+	+	+	+
Ox B		+	+	+	+
Screen			—	+	+
Man				+	+
Sheep					+

Table 1*c*

Total (male and female) *G. pallidipes* caught off

	Dog	Ox B	Screen	Man	Domestic pig	Sheep	Baboon	Goat	Serval cat
Ox A	—	—	+	+	+	+	+	+	+
Dog		—	—	+	+	+	+	+	+
Ox B			+	+	+	+	+	+	+
Screen				—	+	+	+	+	+
Man					—	—	—	—	+
Pig						—	—	—	+
Sheep							—	—	+
Baboon								—	—
Goat									$P=0·2$

Table 2. *Total (males and females) per round*

Screen	Observations	Area sq.m.	Arithmetic mean	Geometric mean
'Scented'	44	2	3·98	3·10
Large	33	2	3·39	2·30
Small	20	1·5	1·50	0·89

Table 3. *Hourly catches (both sexes) from January to October* 1939

	Ox A	Domestic pig	Sheep	Goat	Baboon
No. of hours ...	47	27	41	36	30
Total males	502	78	73	38	14
Arithmetic mean	10·68	2·89	1·78	1·06	0·47
Geometric mean	6·41	2·09	1·06	0·64	0·31
Total females	706	69	11	12	5
Arithmetic mean	15·02	2·56	0·27	0·33	0·17
Geometric mean	8·81	1·64	0·20	0·23	0·12
Females as percentage of total catch	58·5	47·9	13·1	24·0	26·3

Table 4. *Direct comparative catches, March to July* 1940

Animals compared	Observations (hours)	Total (male and female) caught	Significance (χ^2 test)
Porcupine	7½	22	—
Ox B		20	
Ox B		365	
Sheep	55	25	+
Ox B		416	
Goat	25	21	+
Ox B		54	
Domestic pig	10	24	+
Domestic pig		35	
Goat	10	17	+
Domestic pig		31	
Sheep	15	8	+
Domestic pig		63	
Baboon	10	3	+
Sheep		22	
Baboon	15	3	+
Ox B		19	
Greater kudu (young)	2½	3	+

for the moving rounds, since it refused to stand still at intervals and allow the flies to be caught on it. All the bait animals used on these stationary catches had been carefully trained prior to use in these observations, and the wild animals had been hand reared and were very tame. It is probable that the docility of the bait used has a considerable effect on the results.

5. ADVANTAGES OF STATIONARY CATCHES

Both methods show significant differences between certain of the various baits used; however, stationary catches are to be preferred because (*a*) two or more baits can be directly compared, by stationing them a few yards apart and interchanging positions at regular intervals. This also eliminates the activity factor caused by changing climatic conditions and time of day, together with any lunar effect on catches done on different days (Vanderplank, 1941). (*b*) Moving catches are suspected of taking a proportion of non-hungry males that would normally be inactive but are attracted to a moving object (passing within sight of their resting place) irrespective of its nature. Any flies that are collected on the way to and immediately after arriving at the site for a stationary catch are recorded but disregarded, so that all the tsetses caught during the time that the bait is tethered have to be sufficiently active to find and come to the animal.

6. SUMMARY

1. A description of the area in which these experiments have been carried out is given and accompanied by a map. Swynnerton (1936) has described this area and its history, but changes have taken place since his account was written.

2. Tables 1 and 1 *a–c* show the number of observations (rounds), and the arithmetic and geometric mean catches of male and female *Glossina pallidipes*, on two oxen, a screen, man, sheep, goat, baboon, domestic pig, dog, and serval cat used on moving rounds; and the significant differences between them.

3. Observations with three different types of T screens are described (Table 2). A bush-pig scented screen, although it caught slightly more flies, was not significantly more attractive than an unscented screen of the same size;* however, both these screens caught significantly more than did one the same shape and colour but three-quarters the total area of either.

4. A second method of catching on tethered animals is described (stationary catches). Table 3 shows the number of observations, arithmetic and geometric mean catches, on ox, domestic pig, sheep, goat and baboon, of both male and female flies.

5. Certain other baits used for short periods, namely Thomson's gazelle, reedbuck, serval cat and two lion cubs, took only very few flies.

6. A series of direct comparisons (Table 4) with pairs of different baits were carried out and the results tested by χ^2. Catches on porcupine were not significantly different from those on ox. Ox and sheep, ox and goat, ox and domestic pig, domestic pig and goat, domestic pig and sheep, domestic pig and baboon, sheep and baboon, ox and kudu all gave significantly different catches.

* See footnote on p. 41.

7. CONCLUSION

Glossina pallidipes (Aust.) has been noted in the past by various observers for its reluctance to come to man, showing preferences for certain baits. Baits tested were, in order of attractiveness: (1) dog, ox and porcupine, (2) domestic pig and screen, (3) sheep, goat, man, baboon, (4) serval cat, lion, jackal. Data are insufficient to place the other baits used.

8. ACKNOWLEDGEMENTS

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SCIENTIFIC NAMES OF WILD ANIMALS MENTIONED IN TEXT

Thomson's gazelle	*Gazella thomsoni* Gunthr.	Lion	*Panthera leo* L.
Reedbuck	*Redunca redunca* Pall.	Serval cat	*Leptailurus serval* Schreber
Greater kudu	*Strepsiceros strepsiceros* Pall.	Jackal	*Canis mesomelas* Schreber
Bush-pig	*Potamochoerus kioropotamus* Desmoulins	Porcupine	*Hystrix africae-australis* Ptrs.

REFERENCES

Harris, R. H. T. P. (1930). 'Report on the bionomics of the tsetse fly (*Glossina pallidipes* Aust.) and a preliminary report on a new method of control, presented to the Provincial Administration of Natal.' Fol. 75 pp. Pietermeritzburg.

Jack, R. W. (1941). 'Notes on the behaviour of *Glossina pallidipes* and *G. brevipalpis*, and some comparisons with *G. morsitans*.' Bull. Ent. Res. 31: 407–30.

Jackson, C. H. N. (1937). 'Some new methods in the study of *Glossina morsitans*.' Proc. Zool. Soc. Lond.: 811–96.

Lloyd, H. M. (1935). 'Notes on the bionomics of *Glossina swynnertoni*, Austen.' Bull. Ent. Res. 26: 439–68.

Swynnerton, C. F. M. (1921). 'An examination of the tsetse problem in North Mossurise, Portuguese East Africa.' Bull. Ent. Res. 11: 315–85.

Swynnerton, C. F. M. (1936). 'The tsetse flies of East Africa, a first study of their ecology, with a view to their control.' Trans. R. Ent. Soc. Lond. 84: i–xxxi, 1–579 (especially pp. 316–18).

Vanderplank, F. L. (1941). 'Activity of *Glossina pallipides* and the lunar cycle (Diptera).' Proc. R. Ent. Soc., Lond. (A) 16: 61–4.

Williams, C. B. (1937). 'The use of logarithms in the interpretation of certain entomological problems.' Ann. Appl. Biol. 24: 404–14.

Williams, C. B. (1940). 'An analysis of four years captures of insects in a light trap. Part II. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population.' Trans. R. Ent. Soc. Lond. 90: 227–306.

APPENDIX I

Summarized original data of catches of G. pallidipes *off various baits from moving rounds. January to September* 1939

A. *Catches of male* pallidipes

Catches of male *pallidipes* off

Ox A

1	2	3	4
0	4	—	—
1	6	1·80	0·540
2	2	0·96	0·460
3	1	0·60	0·360
4	2	1·40	0·980
5	3	2·34	1·824
6	1	0·85	0·722
7	1	0·90	0·810
8	2	1·90	1·804
9	1	1·00	1·000
24	1	1·40	1·960
	24	13·15	10·460

Mean = 0·5479

Ox B

1	2	3	4
0	5	—	—
1	4	1·20	0·360
2	3	1·44	0·690
3	2	1·20	0·720
4	4	2·80	1·960
5	2	1·56	1·216
6	2	1·70	1·444
8	1	0·95	0·902
9	1	1·00	1·000
13	1	1·15	1·323
	25	13·00	9·615

Mean = 0·5200

Screen

1	2	3	4
0	30	—	—
1	23	6·90	2·070
2	12	5·76	2·760
3	7	4·20	2·520
4	6	4·20	2·940
5	1	0·78	0·608
6	2	1·70	1·444
8	1	0·95	0·902
9	2	2·00	2·000
10	4	4·16	4·328
11	1	1·08	1·166
15	1	1·20	1·440
17	1	1·25	1·563
21	1	1·34	1·796
	92	35·52	25·537

Mean = 0·3842

Explanation of columns:

Col. 1 is the number of flies (male, female or total) taken in each observation.

Col. 2 is the number of observations or rounds.

Col. 3 is the number in col. 1 plus one unit converted into logarithms and multiplied by the number of observations in col. 2.

Col. 4 is the log of the catch, plus one, squared and multiplied by the number of observations in col. 2.

Means given below are the arithmetic mean of the sum of log catches.

Catches of male *pallidipes* off

Man

1	2	3	4
0	20	—	—
1	6	1·80	0·540
2	6	2·88	1·380
3	2	1·20	0·720
5	1	0·78	0·608
6	1	0·85	0·722
8	1	0·95	0·902
9	1	1·00	1·000
10	1	1·04	1·082
11	1	1·08	1·166
12	2	2·22	2·464
14	1	1·18	1·369
	43	14·98	11·953

Mean = 0·3475

Sheep

1	2	3	4
0	20	—	—
1	7	2·10	0·630
2	6	2·88	1·380
3	6	3·60	2·160
4	1	0·70	0·490
7	1	0·90	0·810
8	1	0·95	0·902
10	1	1·04	1·082
	43	12·17	7·454

Mean = 0·2830

Goat

1	2	3	4
0	23	—	—
1	7	2·10	0·630
2	8	3·84	1·840
3	2	1·20	0·720
5	2	1·56	1·216
7	2	1·80	1·620
8	1	0·95	0·902
	45	11·45	6·928

Mean = 0·2545

Serval cat

1	2	3	4
0	5	—	—
1	3	0·90	0·270
2	1	0·48	0·230
	9	1·38	0·500

Mean = 0·1533

Catches of male *pallidipes* off

Baboon

1	2	3	4
0	24	—	—
1	4	1·20	0·360
2	1	0·48	0·230
3	4	2·40	1·440
6	2	1·70	1·444
7	1	0·90	0·810
8	2	1·90	1·804
9	1	1·00	1·000
16	1	1·23	1·513
	40	10·81	8·601

Mean = 0·2703

Domestic pig

1	2	3	4
0	22	—	—
1	5	1·50	0·450
2	6	2·88	1·380
3	3	1·80	1·080
4	2	1·40	0·980
5	1	0·78	0·608
6	1	0·85	0·722
7	2	1·80	1·620
8	1	0·95	0·902
10	1	1·04	1·082
	44	13·00	8·824

Mean = 0·2954

Dog

1	2	3	4
0	0	—	—
1	3	0·90	0·270
2	3	1·44	0·690
3	3	1·80	1·080
4	1	0·70	0·490
6	1	0·85	0·722
10	1	1·04	1·082
	12	6·73	4·334

Mean = 0·5608

B. *Catches of female* pallidipes

Catches of female *pallidipes* off

Ox A

1	2	3	4
0	10	—	—
1	3	0·90	0·270
2	6	2·88	1·380
3	2	1·20	0·720
4	1	0·70	0·490
5	1	0·78	0·608
29	1	1·48	2·190
	24	7·94	5·658

Mean = 0·3309

Ox B

1	2	3	4
0	10	—	—
1	8	2·40	0·720
2	5	2·40	1·150
4	1	0·70	0·490
5	1	0·78	0·608
	25	6·28	2·968

Mean = 0·2513

Screen

1	2	3	4
0	71	—	—
1	11	3·30	0·990
2	6	2·88	1·380
3	2	1·20	0·720
4	1	0·70	0·490
7	1	0·90	0·810
	92	8·98	4·390

Mean = 0·0976

Catches of female *pallidipes* off

Domestic pig

1	2	3	4
0	39	—	—
1	3	0·90	0·270
2	2	0·96	0·460
	44	1·86	0·730

Mean = 0·0423

Man

1	2	3	4
0	41	—	—
1	2	0·60	0·180
	43	0·60	0·180

Mean = 0·0139

Sheep

1	2	3	4
0	39	—	—
1	4	1·20	0·360
	43	1·20	0·360

Mean = 0·0279

C. *Catches of total* (*male and female*) pallidipes

Catches of total *pallidipes* off

Ox A

1	2	3	4
0	1	—	—
1	5	1·50	0·450
2	2	0·96	0·460
3	4	2·40	1·440
4	3	2·10	1·470
5	1	0·78	0·608
7	2	1·80	1·620
8	1	0·95	0·902
9	2	2·00	2·000
12	1	1·11	1·232
14	1	1·18	1·369
53	1	1·73	2·993
	24	16·41	14·544

Mean = 0·6837

Ox B

1	2	3	4
0	2	—	—
1	6	1·80	0·540
2	1	0·48	0·230
3	4	2·40	1·440
4	1	0·70	0·490
5	2	1·56	1·216
6	3	2·55	2·166
7	2	1·80	1·620
9	2	2·00	2·000
10	1	1·04	1·082
13	1	1·15	1·323
	25	15·48	12·107

Mean = 0·6191

Screen

1	2	3	4
0	23	—	—
1	22	6·60	1·980
2	10	4·80	2·300
3	12	7·20	4·020
4	7	4·90	3·430
5	3	2·34	1·824
6	3	2·55	2·166
7	1	0·90	0·810
8	1	0·95	0·902
9	2	2·00	2·000
10	4	4·16	4·328
13	1	1·15	1·323
15	1	1·20	1·440
18	1	1·28	1·638
21	1	1·34	1·796
	92	41·37	29·957

Mean = 0·4496

Catches of total (male and female) *pallidipes* off

Man

1	2	3	4
0	18	—	—
1	8	2·40	0·720
2	6	2·88	1·380
3	2	1·20	0·720
5	1	0·78	0·608
6	1	0·85	0·722
8	1	0·95	0·902
9	1	1·00	1·000
10	1	1·04	1·082
11	1	1·08	1·666
12	2	2·22	2·464
14	1	1·18	1·369
	43	15·58	12·133

Mean = 0·3622

Sheep

1	2	3	4
0	17	—	—
1	10	3·00	0·900
2	6	2·88	1·380
3	6	3·60	2·160
4	1	0·70	0·490
7	1	0·90	0·810
8	1	0·95	0·902
11	1	1·08	1·166
	43	13·11	7·808

Mean = 0·3049

Domestic pig

1	2	3	4
0	17	—	—
1	8	2·40	0·720
2	8	3·84	1·816
3	3	1·80	1·080
4	2	1·40	0·980
5	1	0·78	0·608
6	1	0·85	0·722
7	2	1·80	1·620
8	1	0·95	0·902
10	1	1·04	1·082
	44	14·86	9·530

Mean = 0·3378

Only one female was caught off goat and none off dog, serval cat or baboon. Therefore see data for male *pallidipes* under these baits.

D. *Summarized data from three comparative screens*

Catches of total (male and female) *pallidipes* off

Large unscented screen*

1	2	3	4
0	4	—	—
1	10	3·00	0·900
2	4	1·92	0·920
3	5	3·00	1·800
4	2	1·40	0·980
5	2	1·56	1·216
7	1	0·90	0·810
9	1	1·00	1·000
10	1	1·04	1·082
11	1	1·08	1·166
12	2	2·22	2·464
	33*	17·12	12·338

Mean = 0·5188

Large scented screen

1	2	3	4
0	3	—	—
1	7	2·10	0·630
2	8	3·84	1·840
3	5	3·00	1·800
4	6	4·20	2·940
5	2	1·56	1·216
6	3	2·55	2·166
7	5	4·50	4·050
9	2	2·00	2·000
10	1	1·04	1·082
11	2	2·16	2·332
	44	26·95	20·056

Mean = 0·6125

Small screen

1	2	3	4
0	9	—	—
1	5	1·50	0·450
2	1	0·48	0·230
3	3	1·80	1·080
4	1	0·70	0·490
10	1	1·04	1·082
	20	5·52	3·332

Mean = 0·2760

* These observations are included in the 92 observations shown in Table 1, Appendix I A, B, and are the only ones from that series directly comparable with the scented and small screen catches. The figures in Table 1 and Appendix I A, B are from the first two stages of the round which were the only ones carried out by the animals, and not from the full 3 stages, which were all used in the comparison of the screens.

APPENDIX II

Summarized data from the stationary catches. January to October 1939

A. *Catches of male* pallidipes *per hour*

Catches of male *pallidipes* off

Domestic pig

1	2	3	4
0	4	—	—
1	4	1·20	0·360
2	7	3·36	1·610
3	3	1·80	1·080
4	3	2·10	1·470
5	2	1·56	1·216
6	2	1·70	1·444
7	1	0·90	0·810
10	1	1·04	1·082
	27	13·49	9·072

Mean = 0·4907

Sheep

1	2	3	4
0	16	—	—
1	12	3·60	1·080
2	4	1·92	0·920
3	2	1·20	0·720
4	1	0·70	0·490
5	1	0·78	0·608
6	2	1·70	1·444
7	1	0·90	0·810
9	1	1·00	1·000
10	1	1·04	1·082
	41	12·84	8·154

Mean = 0·3133

Goat

1	2	3	4
0	21	—	—
1	4	1·20	0·360
2	4	1·92	0·920
3	4	2·40	1·440
4	1	0·70	0·490
5	2	1·56	1·216
	36	7·78	4·426

Mean = 0·2161

Catches of male *pallidipes* off

Ox A

1	2	3	4	1	2	3	4
0	4	—	—	11	3	3·24	3·498
1	2	0·60	0·180	12	1	1·11	1·232
2	6	2·88	4·332	18	2	2·56	3·276
3	2	1·20	0·720	23	2	2·76	3·808
4	1	0·70	0·490	24	1	1·40	1·960
5	4	3·12	2·432	27	2	2·90	4·206
6	3	2·55	2·166	32	2	3·04	4·620
7	2	1·80	1·620	36	1	1·57	2·465
8	5	4·75	4·510	54	1	1·74	3·028
9	3	3·00	3·000				
					47	40·92	47·543

Mean = 0·8706

Baboon

1	2	3	4
0	21	—	—
1	5	1·50	0·450
2	3	1·44	0·690
3	1	0·60	0·360
	30	3·54	1·500

Mean = 0·1180

B. *Catches of female* pallidipes *per hour*

Catches of female *pallidipes* off

Ox A

1	2	3	4
0	3	—	—
1	2	0·60	0·180
2	3	1·44	0·460
3	1	0·60	0·360
4	4	2·80	1·920
5	3	2·34	1·824
6	1	0·85	0·722
7	3	2·70	2·430
8	3	2·85	2·706
9	1	1·00	1·000
10	1	1·04	1·082
12	2	2·22	2·464
13	3	3·45	3·969
15	1	1·20	1·440
16	1	1·23	1·513
17	1	1·25	1·563
19	2	2·60	3·386
20	1	1·32	1·742
22	3	4·08	5·550
24	1	1·40	1·960
30	1	1·49	2·220
31	1	1·51	2·280
37	1	1·58	2·496
38	1	1·59	2·528
51	1	1·72	2·958
73	1	1·87	3·497
75	1	1·88	3·534
	47	46·61	56·048

Mean = 0·9917

Domestic pig

1	2	3	4
0	9	—	—
1	4	1·20	0·360
2	3	1·44	0·690
4	5	3·50	2·450
6	4	3·40	2·888
7	1	0·90	0·810
8	1	0·95	0·902
	27	11·39	8·100

Mean = 0·4215

Sheep

1	2	3	4
0	30	—	—
1	11	3·30	0·990
	41	3·30	0·990

Mean = 0·0805

Baboon

1	2	3	4
0	25	—	—
1	5	1·50	0·450
	30	1·50	0·450

Mean = 0·0500

Goat

1	2	3	4
0	27	—	—
1	7	2·10	0·630
2	1	0·48	0·230
3	1	0·60	0·360
	36	3·18	1·220

Mean = 0·0883

All the data for Table 4 in text are given in that table.

THE BREEDING DISTRIBUTION, HISTORY AND POPULATION OF THE NORTH ATLANTIC GANNET (*SULA BASSANA*)

PART 2. THE CHANGES IN THE WORLD NUMBERS OF THE GANNET IN A CENTURY

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(With 4 Figures in the Text)

CONTENTS

1. INTRODUCTION

Part 1 of this paper (4) has been devoted to a description of the history of the North Atlantic gannet (*Sula bassana* L.) at each of the thirty-nine places where it breeds, has bred, has been suspected to have bred, or has occupied suitable nesting-sites in the breeding season. It has dealt, particularly, with the attempt to visit the colonies existing in 1939, and make counts of the number of pairs occupying nests at those colonies. The account is as full as a thorough search of the literature could make it, and the 1939 census was nearly complete, embracing all but about 2·5 % of the world population.

In Part 1 the colonies were suitably grouped, in the geographical sense; and we shall, in this part of the paper, discuss the population changes and trends in these groups, and in the world range of *Sula bassana*. The nature of early records is such that we cannot begin our study until the early nineteenth century; but from about 1833 onwards population records become progressively more numerous and accurate, and in the discussion and figures that follow we generally begin at this date.

We close our account of the gannet with a discussion of man's influence on its numbers and the nature of its colonies.

2. LOCAL POPULATION TRENDS

In Part 1 the gannet's colonies were divided into six groups: south-west Britain, east Britain, west Britain, north Britain and the Faeroes, Iceland, and the Gulf of St Lawrence. We do not claim that the division between some of those in Britain is more than arbitrary; but it has been found of practical convenience to arrange them so. It is of considerable interest to study the population figures of each of these groups, where necessary with the aid of graphs (Figs. 1–4) of the numbers of breeding pairs at each colony, plotted against time. Since the size of a colony may range from 1 pair to over 100,000 (Bird Rocks, Gulf of St Lawrence, in its early days) it has been necessary to plot numbers on a logarithmic scale. As has been shown elsewhere (3) this is of convenience in determining the existence and duration of colonization of breeding stations from outside.

The counts and estimates upon which the figures are based are described in Part 1. They are recapitulated in summarized form only in this Part.

(a) South-west Britain Group

Colony 1 (Gulland Rock, Cornwall) is omitted from discussion.

Summarized history of population
(figures in pairs)

2. Lundy, Devon

Breeding before 1800, 1829, 1839; decrease 1871; breeding 1883–91; count 16 1887; estimates under 70 1889, 70 1890; breeding 1891; count 30 1893, 3 1900, 7 1901, 5 1903, 0 1904–7; extinct 1909; unsuccessful attempt by pair to breed 1922; unsuccessful attempts at reintroduction 1938, 1939.

3. Grassholm, Pembrokeshire

? breeding 1820; breeding 1860, 1864; count 20 1883, 250 1886; estimate 225 1889, over 200 1890; count 240 1893; estimate 300 1895; breeding 1898; estimate 275 1903; under 300 1905, 115 1906, 300 1907–14; increasing 1919; estimate 900 1922, 1900 1924; increasing 1928; count 4750 1933; increasing 1934; estimate 5000 1937, 5875 1939.

4. Great Orme's Head, Caernarvonshire

Pair present, breeding not proved 1941.

5. Little Skellig, Kerry

Breeding before 1800, 1828; estimate 500 1850; breeding 1869, 1870; estimate 30 1880, 175 1882; increasing 1884; several thousand 1890; many thousands 1896; estimate 17,500 1906, 1908; estimate 8000 1913; increasing 1914; estimate 10,000 1930, 9500 1938, 1939, 1941.

6. Bull Rock, Cork

Present but not breeding 1853; breeding 1856; count 11 1858; many hundreds 1868; estimate under 1000 1884, 500 1889; count 105 1891; decreasing 1896; estimate 100 1899, 1000 1902; count 300 1908, 250 1913, 400 1930; estimate 450 1937, 471 1938, 575 1939.

7. Great Saltee, Wexford

Count 2 1929, 0 1930, 2 1932, 1 1933, 1 1934, 1 1935, 1 1936, 2 1937, 3 1938; not proved present 1939; count 2 1943. (The figure 0, here and in what follows, means present on a suitable nesting-site, but no egg or young proved to have been produced.)

8. Stags of Broadhaven, Mayo

? breeding before 1800, 1823–8, 1836; extinct 1873, 1882, 1898, 1911, 1924, 1928–30, 1939.

Trends in the population of the group

The foregoing summary deals only with observations with a bearing on the population at the colonies in the south-west Britain group. The populations, in pairs occupying nests, are plotted logarithmically in Fig. 1. Other observations, particularly those dealing with the effect of man, that have any bearing on changes in numbers at the different colonies, will be most conveniently found in the summary to each colony's history, in Part 1. At the top of Fig. 1, and the two succeeding figures are indicated the periods during which colonization was certain or probable at the various colonies. Fisher & Venables(**3**) have shown that in a gannet colony an increase at the rate of more than 25 % per annum must be due, at least partly, to colonization from without, and that an increase of more than 12 % per annum means that colonization is probable. All the counts and estimates available, that were judged to have been of reliability, have been used. Some obviously unreliable estimates have been ignored (Part 1 can be studied to see which these were); some others, that have been used, *may* of course be poor, though we have tried to maintain critical standards of judgement (thus the estimates for the population of Little Skellig in 1906 and 1908 *may* be too high, when considered 'in their context' and in the light of world population trends). In three cases we have made bold assumptions, in the absence of definite figures; to Little Skellig ('several thousands') 1890 we have assigned the figure 2000, to the same colony ('many thousands') 1896 the figure 5000, and to Bull Rock ('many hundreds') 1868 the figure 500.

To establish the trend of world population (see p. 56) it has been necessary to trace gannet numbers, where possible, back to 1833, chosen as the year of Audubon's visit to the Bird Rocks, which at that time held about twice as many gannets as the rest of the world's colonies put together. The colonies of Little Skellig and Lundy alone certainly existed at that time; Grassholm may have held some gannets

General caption to Figs. 1–3

Colonization certain (increase of 25 % or more per year) during period embraced.

Colonization probable (increase of 12 % or more per year) during period embraced.

---------- Population of colony assigned, in this period, to earliest (or latest) known figure.

–·–·–·–·–·–·– Existence of colony probable, but not proved, in this period.

+ + + + + + + Colony in existence; plot on graph has special explanation in text.

+·+·+·+·+ Existence of colony probable, but not proved; plot on graph has special explanation in text.

Unbroken line: Connects all plotted points (where counts or estimates are considered reliable); it is not claimed that it directly represents the situation in the colony in years for which there is not observation and hence no plot. Stars plotted *below* abscissa represent birds present but no pair proved to lay egg.

Ordinate: Number of pairs breeding at the colonies, plotted on logarithmic scale.

Abscissa: Years from 1833, or later, to 1942.

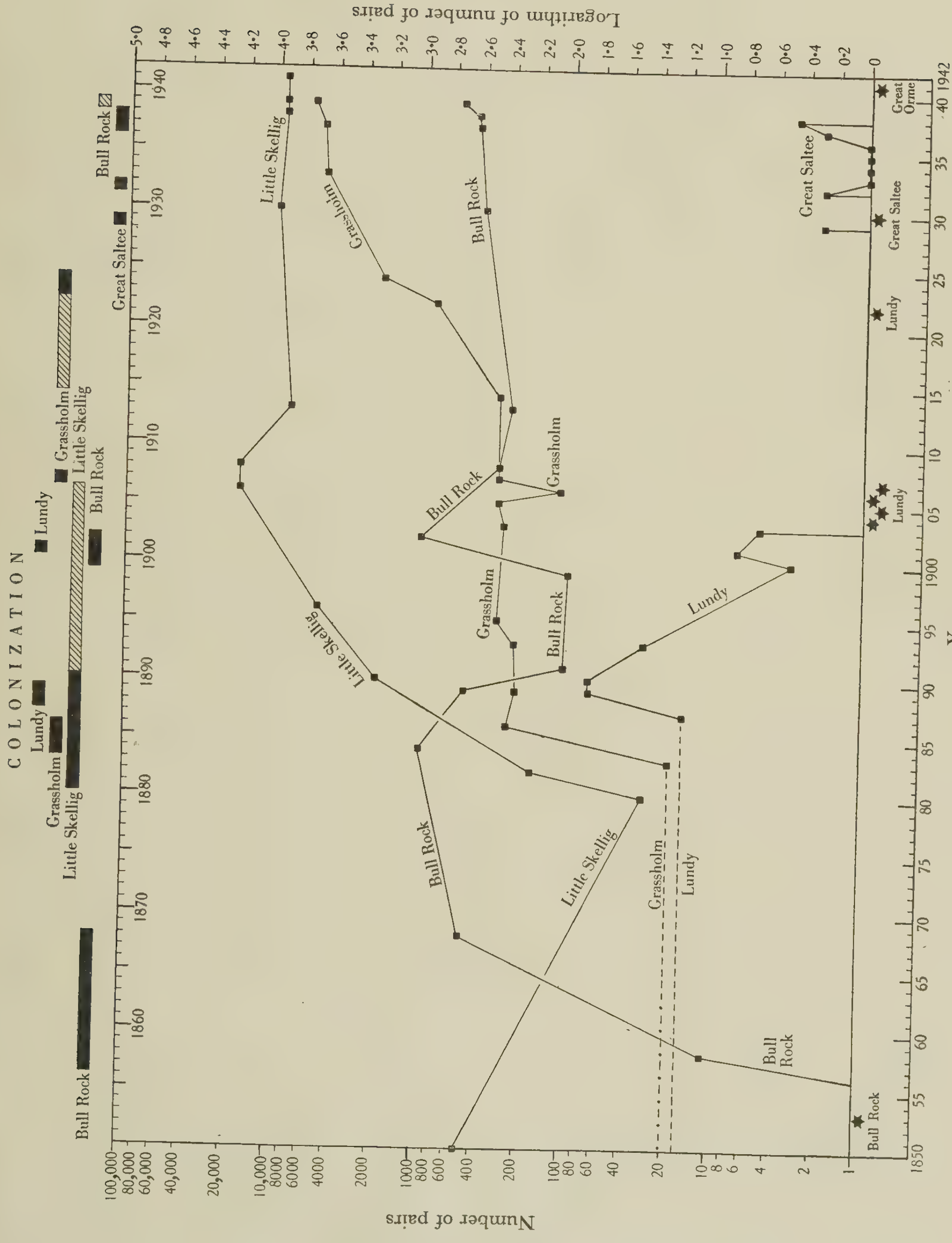

Fig. 1. The population (in pairs) of the colonies in the south-west Britain group, 1850–1942.

then; the history of the possible colony on the Stags of Broadhaven at that time is doubtful (and it is not plotted on the graph); and there was no colony, as far as is known, in 1833 at the Bull Rock or Great Saltee. But from Little Skellig, Lundy and Grassholm we have no contemporary figures; so we have assigned to them, for the period between 1833 and the year in which we have the earliest figure, the figure in that year. We have done the same, for other colonies in other groups, for which the earliest figures are not available until after 1833.

One of us has already published a discussion of trends in the south-west Britain group (**2**). This discussion mainly dealt with the evidence for interchange between the different colonies in the group, from the period in which the Bull Rock colony was established, onwards; but it did not stress the remarkable changes that the population, as a whole, has suffered in this group.

Even if we omit the high figures for Little Skellig in 1906 and 1908, which may be too high, we find a steady trend towards increase among the total population of gannets in the south-west Britain group which is practically continuous from about 1859, when it was at its lowest, to the present day. From such figures as we have, it would seem that there were no more than between 200 and 300 pairs of gannets, altogether, in this group in 1859; in 1939 there were nearly 16,000—owing to the great rise of Little Skellig. In eighty years the gannets have increased sixty-fold.

There is no doubt that the south-west Britain group has been colonized from outside, particularly in the last twenty years of the nineteenth century. There is no doubt, too, that a large proportion of the increase has been due to the releasing of the dominating colony of Little Skellig from the pressure of the gannet's chief predator, man. (Man's influence on gannet numbers is discussed generally in § 4 (p. 58).)

In Part 1 (p. 178) we show that young were taken at Little Skellig in 1850, and that by 1869 the rock was still rented for the taking of gannet's feathers and young. This was all the information, about human predation, that we had at the time of publication of Part 1. Since then further information has come to light. In about 1878 (**6**) Tomás ó Crohan, who lived all his life on Great Blasket, was told by an older friend John Dunlevy that 'All the gannets hatch on the smallest of the Skelligs, and you never saw anything like the crowds of young birds there. A boat with a crew of twelve men used to be guarding the rock, well paid by the man who owned it.' Some time in the early nineteenth century (it is impossible to discover, from the book, even approximately when) a rival boat of eight men sailed to Little Skellig from the little harbour of Dunquin, and got a boatload of young birds from the rock. They were boarded by the crew of the guard boat, and in the fight that resulted two of the guards were killed 'and the rest were sent into hospital. After that they were less keen on that sort of chase and the guard was taken off the rock, and those birds are no longer eaten in these days'.

From this account it is clear that gannet taking was, to say the least of it, important in the early days of the nineteenth century. When it stopped we are unable to discover. But it had stopped when John Dunlevy told this tale to ó Crohan, in about 1878. And from 1880 onwards Little Skellig was rapidly colonized, rising from about 30 pairs (1880) to perhaps 17,500 (1906) in 26 years.

In the previous discussion (**2**) of the changes in population in the south-west Britain group, one of us stated: 'To-day it seems, from observers' accounts, that Little Skellig and the Bull Rock have nearly reached saturation point, while Grassholm cannot be very far off it.' This statement can be regarded as too sweeping; but undoubtedly the recent increases in the colonies at Grassholm and Bull Rock can be regarded as minor changes. Yet there is certainly room for considerably more gannets on Grassholm and probably room for more on the Bull Rock and Little Skellig (especially if it is true that there were about 17,500 pairs on Little Skellig in 1906 and 1908). The attempts by a very few pairs of gannets to establish a colony on Great Saltee do not seem to be meeting with success; new gannet colonies (e.g. Noss, Hermaness, Scar Rocks) have been formed very much more swiftly than this.

(*b*) East Britain group

Summarized history of population
(figures in pairs)

9. Bempton Cliffs, Yorkshire

0 1924–6, 1928–9; count 1 1937, 2 1938, 4 1939; 0 1940–2.

10. Bass Rock, East Lothian

Breeding before 1800; estimate 10,000 1831, 5000 1847 or 1848, 3400 1850, 6000 1869; increasing 1873; estimate 3000 1904; increasing 1909; estimate 3250 1913; count 4147 1929; estimate 4150 1936; count 4374 1939.

11. Isle of May, Fife

Breeding before 1850, 0 1922.

Trends in the population of the group

The historic colony at the Bass Rock has, it would appear, had a remarkable steady population during the period under review. Although serious economic exploitation by man had ceased by 1885, there appears to have been a decrease during the last quarter of the nineteenth century. This is based

on the figures and on observations of the area occupied. The colony did not recover from this not very serious set-back until about 1909. To-day, though the population is relatively high, the gannets are not breeding to any extent on the slopes above the cliffs. Provided the birds are undisturbed, this area is still available for them to exploit. A general impression from a study of the considerable history of this colony is that during the period under review the population has usually approached saturation on the cliff ledges.

The new colony on Bempton Cliffs, which can be presumed to be an offshoot of that on the Bass Rock, has had a history in many ways like that at Great Saltee. It does not, yet, appear to have got going.

The population (in pairs) of the colonies in the east Britain group, 1831–1942, is plotted in Fig. 4.

(*c*) WEST BRITAIN GROUP

Colonies 15–17 (Islay, Eigg and Rum) are omitted from discussion.

Summarized history of population
(figures in pairs)

12. Calf of Man, Isle of Man

Possibly breeding *c.* 1652; 0 1939.

13. Scar Rocks, Luce Bay, Wigtownshire

Count 2 1883; probably not present 1884–1938; count 1 1939; present 1940; estimate 10 1941, 25 1942, 45 1943.

14. Ailsa Craig, Ayrshire

Breeding before 1800, 1813, 1850; estimate 7500 1868, 6000 1869, 3250 1905; increasing 1913; estimate 4900 1922; increasing 1923; estimate 8000 1924; increasing 1925; estimate 7000 1929, 1935; count 4800 1936; estimate 5945 1937; count 5387 1938, 5419 1939, 6232 1940, 3518 1941, 4829 1942.

Trends in the population of the group

Like the colony at the Bass Rock, that at Ailsa Craig appears, on the whole, to have had a steady population during the period under review. But, as the study in detail of recent changes in its population shows, there is a considerable amount of fluctuation in numbers from year to year around a mean (1935–42) of about 5400 pairs. The fluctuation has been such that in two years (1937 and 1940) there was the appearance of probable colonization from without, with increases of over 12 % on the number in the previous year; and in 1942 certain colonization, the increase being over 25 %. We cannot discard the possibility that these colonizations may have been by birds that did not breed in the previous year, rather than by birds from another colony.

The return of gannets to the Calf of Man, after an apparent interval of nearly 300 years, is interesting; but they have shown no very definite signs of breeding. The new colonization at the Scar Rocks, from 1939 onwards, is more interesting, particularly as it appears to be well established and rapid; its further development may be affected by certain factors which cannot at the moment be discussed.

As has been shown in Part 1 of this paper, there is certainly room for a considerably larger population of gannets on Ailsa Craig. The cliffs can hold at least 8000 pairs without the birds spreading on to the sloping, broken ground at their tops. The Scar Rocks are small, and cannot hold a very large number of gannets, though McWilliam(5) says that they can easily hold hundreds.

Serious exploitation by man of the gannets on Ailsa Craig has not been recorded after *c.* 1880, or possibly 1871.

The population (in pairs) of the colonies in the west Britain group, 1868–1942, is plotted in Fig. 4.

(*d*) NORTH BRITAIN-FAEROES GROUP

Colonies 18 (Oigh-sgeir Eagach), 20 (Rockall) and 22 (North Rona) are omitted from discussion.

Summarized history of population
(figures in pairs)

19. St Kilda, Inverness

Breeding before 1800, 1829, 1869; estimate 14,750 1902, 16,500 1931; count 16,900 1939.

21. Sula Sgeir, Outer Hebrides, Ross

Breeding before 1800, 1869; estimate 7000 1884, over 5000 1887, 5000 1932; count 4418 1937, 3970 1939.

23. Sule Stack, Orkney

Breeding before 1800, 1869; estimate 3500 1890, 4000 *c.* 1904, 4000 1914; count 3418 1937, 3490 1939.

24. Copinsay, Orkney

0 1907 or 1908, *c.* 1911 and 1925 or 1926.

25. Noss, Shetland

0 1911 or 1912; count 1 1914, 4 1915, 5 1919, 10 1920; estimate 200 1930 or 1931, 800 1934 or 1935, over 913 1937; count 1518 1938, 1830 1939.

26. Hermaness, Shetland

Breeding 1917; estimate over 109 1920; increase 1928, 1932; estimate over 600 1934, 1000 1935; count 2045 1938, 2611 1939.

27. Myggenaes Holm, Faeroes

Breeding before 1800; estimate 750 1892, 1928, 900 1935; count 1615 1937, 1645 1938, 1473 1939.

Trends in the population of the group

The remarkable development of the two Shetland colonies at Noss and Hermaneness, from nothing to major size in under 30 years, has been the feature of this group. Apart from these there is nothing to great central colony of St Kilda, the largest in the world since the decline of Bird Rocks, has scarcely changed in numbers at all since 1901, the earliest year in which we have a reliable estimate.

At St Kilda predation by man was not so regular

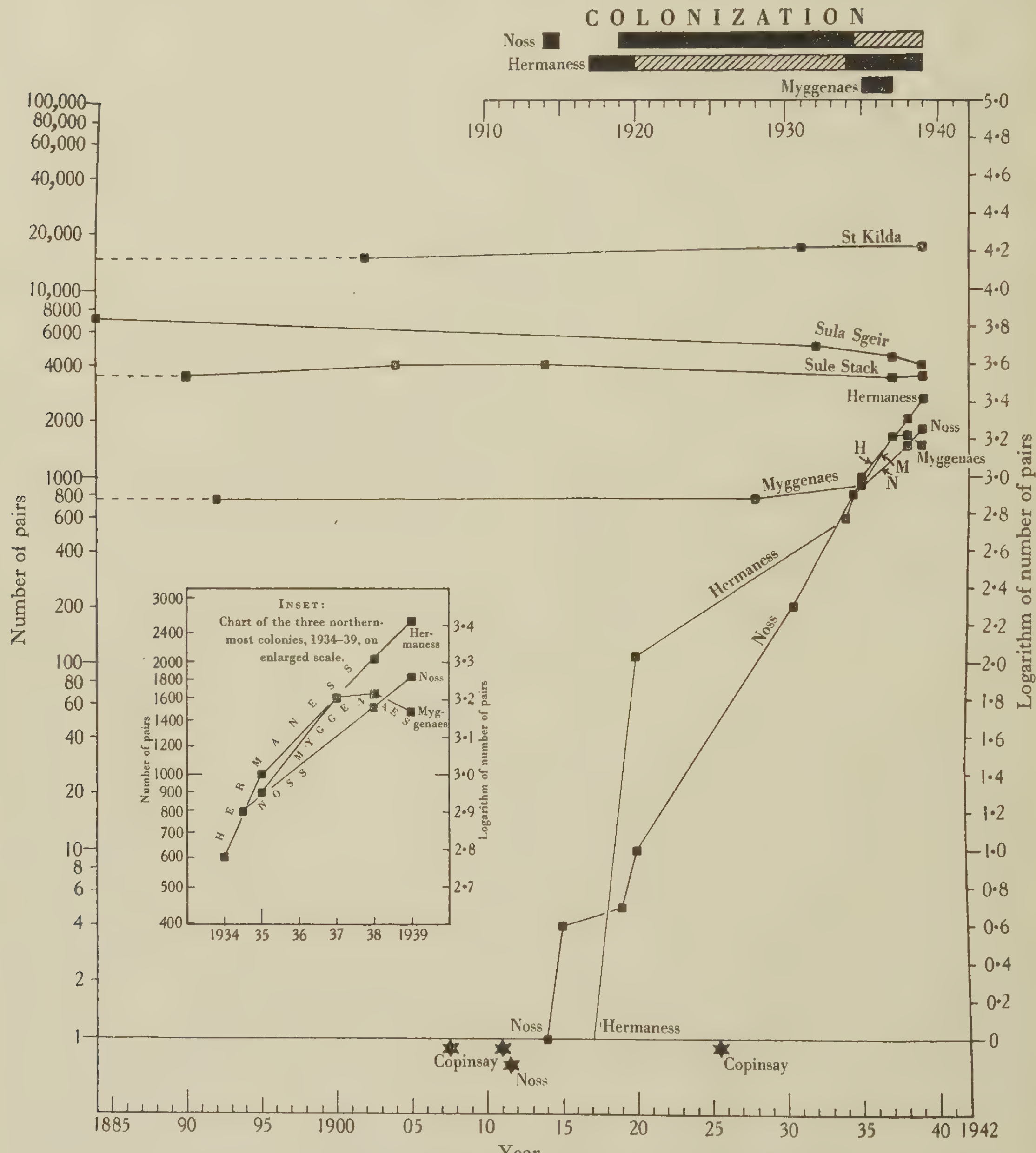

Fig. 2. The population (in pairs) of the colonies in the north Britain-Faeroes group, 1884–1942.

indicate any fundamental change in the size of the colonies save at Sula Sgeir, where there has been a trend towards decrease in recent years. This particular trend cannot yet be regarded as serious. The or serious as has been sometimes supposed, and it is doubtful whether as much as an eighth of the annual production of young was killed in any but a few of the last hundred years. By the twentieth century very

few birds were taken, and there is no evidence of human predation, on an organized scale, after 1910. Sule Stack was periodically raided by the men from Ness in Lewis up to about 1932, but by no means in every year. Sula Sgeir has, however, been raided in most years and is the only place in Great Britain where gannets are taken in large numbers to-day. At Myggenaes, in the Faeroes, a large proportion of the annual production of young is taken every year, as it has been, annually, since at least 1782.

The Shetland colonies have been steadily colonized since they began in 1914 and 1917. Nobody has been able to find the precise origin of their present inhabitants; speculation alone is possible, and should be guarded (and perhaps guided) by the fact that there is certainly room for more breeding gannets on St Kilda and (at the present day) Sula Sgeir, but probably little room for more on Sule Stack. Indeed, with the exception of Eldey, Sule Stack is the only colony which either of us has seen which gives the immediate and convincing impression of being full up.

(*e*) Iceland group

Summarized history of population
(figures in pairs)

28. Westmann Islands

Breeding before 1800; estimate 2000 1898, 5000 1919, 3514 1932, 4000 1935; count 4359 1939.

29. Eldey

Breeding 1821; estimate 10,000 1894, 1904, 1919, 9000 1934; count 9328 1939; estimate over 9000 1941, 1942.

30. Grímsey

Count 14 1819; estimate 20 1820, 60 1903; count 21 1933, 11 1934, 45 1939.

Trends in the population of the group

We know nothing of the gannet population on Eldey before 1894 and the Westmann Islands before 1898. In the twentieth century Eldey appears to had a constant population, while at the Westmann Islands the population appears to have roughly doubled; this in spite of regular annual harvesting of a mean (1913–30) of 478 young gannets, organized by the inhabitants of the islands and taxed by the Government. Grímsey has always been a small colony, interesting because it is within the Arctic Circle, and has been disturbed by seismic movements.

After Sule Stack, Eldey most nearly gives the impression of being full up with gannets (see Part 1, p. 200 and Pl. 9, photo 14). It has been annually harvested up to 1939; the mean annual catch, according to the Government records, was 3257 from 1910 to 1939. In 1940 it was declared a bird sanctuary and gannet-taking forbidden. If the gannets are not disturbed in future years there will, beyond doubt, arise a surplus of birds for which there will be no room on the already crowded top of this remarkable stack; and it will be interesting to see if the Westmann Islands, or other (perhaps new) stations are colonized.

The population (in pairs) of the colonies in the Iceland group, 1833–1942, was plotted on a graph to arrive at figures for Table 1. Since the relevant trends in the population of the colonies in this group can be realized directly and simply by a study of the figures, this graph is not published.

(*f*) St Lawrence group

Summarized history of population
(figures in pairs)

31. Gannet Rock, Grand Manan, New Brunswick

Breeding *c.* 1830; decrease 1831; count 2 1859; extinct 1871.

32. Gannet Rock, Yarmouth, Nova Scotia

Count 150 1856; extinct by 1883.

33. Bird Rocks, Magdalen Islands, Quebec

Breeding before 1800; estimate 112,500 1833, 75,000 1860, 65,000 1864, 27,500 1872, 25,000 1881, 5000 1887, 750 1898, 1500 1904, 500 1932, 1250 1934.

34. Bonaventure Island, Gaspé, Quebec

Breeding 1860; increasing 1883; estimate 1500 1887, 3500 1898, 4000 1914, 1915, 1919; increasing 1923–5; estimate 6000 1932, 6500 1934, 7000 1938, 6800 1939, 6680 1940.

35. Perroquet Islands, Mingans, Quebec

Breeding 1857; 'hundreds' 1881; decreasing 1884; 0 1887; extinct 1909.

36. Gull-cliff Bay, Anticosti Island, Quebec

0 1913; breeding 1919 or 1920; over 100 1923; estimate 500 1928; count 496 1940.

37. Cape St Mary, Avalon, Newfoundland

Count 3 1879, 9 1883; increasing 1890; estimate 2000 1913; 3200 1924; increasing 1931; estimate 4000 1934; count 4294 1939.

38. Bacalieu Island, Newfoundland

Possibly breeding since 1901; estimate 200 1941.

39. Funk Island, Newfoundland

Breeding 1534; breeding not proved 1857; extinct 1873, 1887, 1934; count 7 1936.

Trends in the population of the group

Until the eighties of the last century, the colony on the Bird Rocks was the dominant gannet colony in the world, and by far the largest. In 1833 it held about twice as many gannets as the rest of the world, if our method of arriving at its population in that year (see Part 1, p. 202) is approximately correct. But the Newfoundland Banks fishermen, and their colleagues, did not harvest its gannets so much as savage them, wantonly, with the result that by 1887 it had become a colony of normal size by the standards of the others (5000 pairs); and by 1898 it had become small (750). Protective legislation took about 25 years to come into effect, and robbing went on until at least 1900, though probably not to any significant extent after 1904.

The general trend of the west Atlantic population of the gannet is dominated by the history of the Bird Rocks colony until the end of the nineteenth century, when the total population in this group was at its lowest. But before the end of the century interesting developments had taken place at other colonies. Between 1870 and 1887 the two colonies in the Bay of Fundy, and the colony in the Perroquet Islands, were extinguished, probably by savage predation by man; and the colony at Cape St Mary was established and rapidly colonized. The history of the Bonaventure Island colony is well known only from 1887, and quite unknown before 1860; it may well have been established after the colony at Bird Rocks had begun seriously to decrease. Most interesting of all has been the continued colonization of Newfoundland after the establishment of the Cape St Mary colony; in the twentieth century Bacalieu Island has been colonized, and Funk Island recolonized, albeit in small numbers as yet. After a period of rapid colonization, the colony at Gull-cliff Bay, Anticosti, which can reasonably be regarded as an offshoot of the Bird Rocks colony, has remained steady in numbers, with a fairly small population of 500 pairs, for 12 years.

In plotting Fig. 3 we have made certain assumptions about numbers, at certain colonies in certain years, similar to those which we have made in plotting some of the history of the south-west Britain group (p. 52). It must be stressed that these assumptions are made as a basis for plotting the world totals, and the results of the assumptions are such that a very great error cannot influence the world totals to any significant extent or, for that matter, the group totals. Thus we assume that the population at Gannet Rock, Grand Manan, was 40 in 1831, the year in which the lighthouse was built. Part 1 (p. 201) relates that there were one or two pairs nesting in 1859 but more before the lighthouse was built. 40 is our interpretation of 'more than one or two'; though otherwise arbitrary this figure is probably in the correct *order* of numbers. Likewise, we have assigned the figure 400 for the numbers of pairs at the Perroquet Islands in 1881, the year of a great raid by Indians. We know no more about the real figures save that Brewster (see Part 1, p. 205) saw hundreds of gannets nesting. Again, then, the figure we have assigned is probably in the right order of numbers.

3. WORLD POPULATION TRENDS

To establish, and discuss, the nature of world changes in the numbers of the gannet, from Audubon's visit to the Bird Rocks until the present day, we have thought fit to plot curves (Fig. 4) for the total population in each of the six groups, and in the world, from 1829 to 1939. Audubon's visit was in 1833; but we have found it convenient to summarize the situation in every fifth year from 1819 onwards, and plot the curves from 1829 to 1939 with this as a basis (with the exception of the west and east Britain groups, which are so dominated by Ailsa Craig and the Bass Rock that it has sufficed to plot their curves direct from the basic data for these colonies and their tiny satellites).

Table 1 forms the basis for Fig. 4. It has been produced by measuring, from the curves for each colony in Figs. 1–3, and from the unpublished curve of the Iceland colonies, the population in each fifth year, and entering the result correct to two significant figures. The figures for each colony, in each fifth year, are then added to arrive at the total for the group, and these are added to arrive at a total for the world population in that year. It must be stressed that the object has been to establish the nature of the general *trends* of the population; and no claim is made for the exact representation of the situation in any year, save 1939.

The figures in Table 1 show that at the beginning of the period selected, in 1834, the world population was about 170,000 pairs. It steadily declined until in 1894 it reached its lowest at about 53,000 pairs. By 1939 its steady recovery has brought it to about 83,000 pairs.

The figure for 1939 in Table 1 is recorded as 82,755, while the final census figure in Part 1 (p. 208) is 82,801. This is due to the fact that the counts at Gull-cliff Bay (496, 1940) and Bacalieu Island (200, 1941) were added as they stood, to the others, to form the total recorded in Part 1; while for Table 1 the figures for these colonies in 1939 are derived by interpolation; they are, respectively, 500 and 150; to two significant figures.

The limits of error of the 1939 figure have been discussed in Part 1 (p. 207), and the world total of breeding *individuals* in 1939 is considered to be $165{,}600 \pm 9500$.

In the 60 years of steady decrease of the world population (1834–94), the downward trend was primarily due to the fate of the colony on Bird

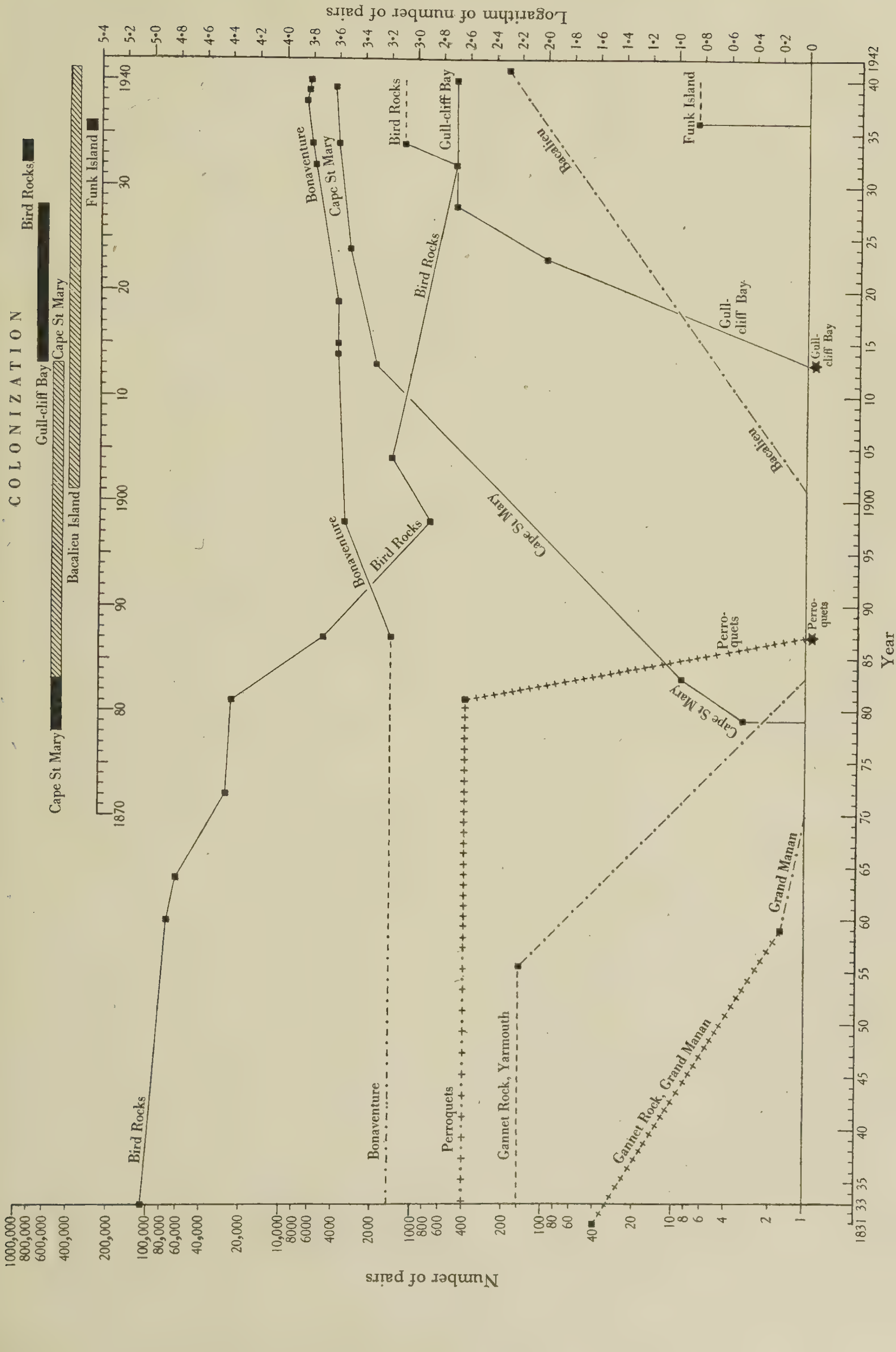

Fig. 3. The population (in pairs) of the colonies in the St Lawrence group, 1833–1942.

Rocks, Magdalen Islands. We know little of trends on the British side of the Atlantic in this period; whatever they were, they cannot have altered the situation significantly, so dominant was the Bird Rocks colony in its early days. We do know, however, that the remarkable upward trend of the south-west Britain group started in about 1864, some time before the world population began to recover. Indeed, while the St Lawrence colonies produced the great decrease, the East Atlantic colonies have produced the recovery. Though the St Lawrence colonies have also recovered, the main part of the increase in the world population from 1894 to the present day is due to the rise of the south-west Britain group and, in recent years, the rise of the Shetland colonies.

In 1834 the St Lawrence colonies held about 67 % of the world population; in 1894 about 8 %; in 1939 about 15·7 %.

In 1864 the south-west Britain colonies held about 0·2 % of the world population; in 1894 about 6 %; in 1939 about 19·3 %.

4. MAN'S INFLUENCE ON GANNET NUMBERS

It will already have been realized that the great decrease of the world's gannets in the nineteenth century was primarily due to the activities of man; and that the twentieth-century recovery is largely due to the relaxation of his predation, to the control of it, or to positive protective measures. In the story of the gannet man appears in the different roles of mass-destroyer, harvester, conservator and protector. When he has indulged in wanton massacre of gannets, such as at the Bird Rocks, probably at Little Skellig in its early days, the world population has seriously suffered. By thoughtless and heedless

Table 1. *The population of the world's gannet colonies, the groups in which they have*

Heavy type: figures established by counts or reliable estimates in the year concerned.
Ordinary type: figures derived from the curves for the colonies (Figs. 1–3) at years lying between those in which there were counts or reliable estimates.

	1819	1824	1829	1834	1839	1844	1849	1854	1859	1864
Lundy	*16*	*16*	*16*	*16*	*16*	*16*	*16*	*16*	*16*	*16*
Grassholm	—	*(20)*	*(20)*	*(20)*	*(20)*	*(20)*	*(20)*	*(20)*	*(20)*	*20*
Little Skellig	*500*	*500*	*500*	*500*	*500*	*500*	*500*	340	210	130
Bull Rock	—	—	—	—	—	—	—	—	16	110
Great Saltee	—	—	—	—	—	—	—	—	—	—
S.W. Britain group: total	516	536	536	536	536	536	536	376	262	276
Bempton Cliffs	—	—	—	—	—	—	—	—	—	—
Bass Rock	*10,000*	*10,000*	*10,000*	8,800	7,200	5,700	4,000	3,800	4,400	5,200
E. Britain group: total	10,000	10,000	10,000	8,800	7,200	5,700	4,000	3,800	4,400	5,200
Scar Rocks	—	—	—	—	—	—	—	—	—	—
Ailsa Craig	*7,500*	*7,500*	*7,500*	*7,500*	*7,500*	*7,500*	*7,500*	*7,500*	*7,500*	*7,500*
W. Britain group: total	7,500	7,500	7,500	7,500	7,500	7,500	7,500	7,500	7,500	7,500
St Kilda	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*
Sula Sgeir	*7,000*	*7,000*	*7,000*	*7,000*	*7,000*	*7,000*	*7,000*	*7,000*	*7,000*	*7,000*
Sule Stack	*3,500*	*3,500*	*3,500*	*3,500*	*3,500*	*3,500*	*3,500*	*3,500*	*3,500*	*3,500*
Noss	—	—	—	—	—	—	—	—	—	—
Hermaness	—	—	—	—	—	—	—	—	—	—
Myggenaes	*750*	*750*	*750*	*750*	*750*	*750*	*750*	*750*	*750*	*750*
N. Britain-Faeroes group: total	26,000	26,000	26,000	26,000	26,000	26,000	26,000	26,000	26,000	26,000
Westmann Islands	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*
Eldey	*10,000*	*10,000*	*10,000*	*10,000*	*10,000*	*10,000*	*10,000*	*10,000*	*10,000*	*10,000*
Grímsey	**14**	21	22	24	26	27	29	31	33	35
Iceland group: total	12,014	12,021	12,022	12,024	12,026	12,027	12,029	12,031	12,033	12,035
Grand Manan	*(40)*	*(40)*	*(40)*	*(28)*	*(16)*	*(9)*	*(5)*	*(3)*	**2**	*(1)*
Yarmouth	*150*	*150*	*150*	*150*	*150*	*150*	*150*	*150*	*(80)*	*(32)*
Bird Rocks	*112,500*	*112,500*	*112,500*	110,000	100,000	96,000	88,000	82,000	76,000	**65,000**
Bonaventure Island	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*	*(1,500)*
Perroquet Islands	(400)	(400)	(400)	(400)	(400)	(400)	(400)	(400)	(400)	(400)
Anticosti Island	—	—	—	—	—	—	—	—	—	—
Cape St Mary	—	—	—	—	—	—	—	—	—	—
Bacalieu Island	—	—	—	—	—	—	—	—	—	—
Funk Island	—	—	—	—	—	—	—	—	—	—
St Lawrence group: total	114,590	114,590	114,590	112,078	102,066	98,059	90,055	84,053	77,982	66,933
World total	170,620	170,647	170,648	166,938	155,328	149,822	140,120	133,770	128,177	117,944

killing man has extinguished at least four colonies in the period under review; Gannet Rock, Grand Manan (1871), Gannet Rock, Yarmouth (1883), the Perroquet Islands (1887) and Lundy (1909). He has endangered the colonies at Grassholm, Little Skellig, and Bird Rocks at certain periods of their history. By mass destruction man reduced the gannet population of the world by about two-thirds in 60 years.

colonies man has acted as an unconscious conservator. Indeed, at Myggenaes the inhabitants carefully plan their takes of birds in each year, and set an upper limit to their bag before they start killing; here we can justifiably call them conscious conservators. At the other colonies it is perhaps the physical circumstances that have prevented man from taking too many; the weather does not permit the men from Ness in Lewis to visit Sula Sgeir in

been arranged, and the total world population in every fifth year from 1819 *to* 1939

Italics: figures which are the same as those recorded in the latest or earliest year of the colony's population history; these could not be established by interpolation (no attempt has been made at extrapolation of the *trends* of colony curves).

Italics in brackets: figures derived from parts of the curves where the existence of the colony is probable, but not proved; or where the plot has a special explanation in the text (see general caption to Figs. 1–3).

1869	1874	1879	1884	1889	1894	1899	1904	1909	1914	1919	1924	1929	1934	1939
16	*16*	*16*	*16*	**70**	22	4	—	—	—	—	—	—	—	—
20	*20*	*20*	46	**225**	260	290	290	**300**	**300**	570	**1,900**	3,200	4,800	**5,875**
84	53	33	320	1,500	3,700	7,300	14,000	15,000	8,100	8,700	9,200	9,800	9,600	**9,500**
520	650	800	**1,000**	**500**	100	**100**	680	290	260	290	340	390	439	**575**
—	—	—	—	—	—	—	—	—	—	—	—	**2**	**1**	—
640	739	869	1,382	2,295	4,082	7,694	15,070	15,590	8,660	9,560	11,440	13,392	14,831	15,950
—	—	—	—	—	—	—	—	—	—	—	—	—	—	**4**
6,000	5,400	4,900	4,500	4,000	3,700	3,300	**3,000**	3,100	3,300	3,600	3,800	**4,147**	4,100	**4,374**
6,000	5,400	4,900	4,500	4,000	3,700	3,300	3,000	3,100	3,300	3,600	3,800	4,417	4,100	4,378
—	—	—	—	—	—	—	—	—	—	—	—	—	—	**1**
6,000	5,500	5,000	4,600	4,300	3,900	3,600	3,300	3,600	4,000	4,500	**8,000**	**7,000**	7,000	**5,419**
6,000	5,500	5,000	4,600	4,300	3,900	3,600	3,300	3,600	4,000	4,500	8,000	7,000	7,000	5,420
14,750	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	*14,750*	15,000	15,000	15,000	16,000	16,000	16,000	17,000	**16,900**
7,000	*7,000*	*7,000*	**7,000**	6,800	6,500	6,300	6,100	5,900	5,700	5,500	5,300	5,100	4,800	**3,970**
3,500	*3,500*	*3,500*	*3,500*	*3,500*	*3,600*	*3,800*	**4,000**	4,000	**4,000**	3,900	3,700	3,600	3,500	**3,490**
—	—	—	—	—	—	—	—	—	**1**	**5**	31	130	660	**1,830**
—	—	—	—	—	—	—	—	—	—	18	180	320	**600**	**2,611**
750	*750*	*750*	*750*	*750*	750	750	750	750	750	750	750	780	880	**1,473**
26,000	26,000	26,000	26,000	25,800	25,600	25,600	25,850	25,650	25,451	26,173	25,961	25,930	27,440	30,274
2,000	*2,000*	*2,000*	*2,000*	*2,000*	*2,000*	2,100	2,600	3,200	4,000	**5,000**	4,400	3,800	3,800	**4,359**
10,000	*10,000*	*10,000*	*10,000*	*10,000*	**10,000**	10,000	**10,000**	10,000	10,000	**10,000**	9,600	9,300	**9,000**	**9,328**
38	41	44	47	50	52	57	58	48	40	34	29	24	**11**	**45**
12,038	12,041	12,044	12,047	12,050	12,052	12,157	12,658	13,248	14,040	15,034	14,029	13,124	12,811	13,732
(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(13)	*(5)*	*(2)*	—	—	—	—	—	—	—	—	—	—	—	—
38,000	27,000	25,000	11,000	3,500	1,500	860	**1,500**	1,200	1,000	840	690	560	**1,250**	*1,250*
(1,500)	*(1,500)*	*(1,500)*	*1,500*	1,800	2,600	3,500	3,700	3,800	**4,000**	**4,000**	4,600	5,500	**6,500**	**6,800**
(400)	*(400)*	*(400)*	*(20)*	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	2	15	140	500	500	500
—	—	**3**	11	26	66	160	400	1,000	2,100	2,600	**3,200**	3,600	**4,000**	**4,294**
—	—	—	—	—	—	—	1	3	5	11	21	41	79	150
—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
39,914	28,905	26,905	12,531	5,326	4,166	4,520	5,601	6,003	7,107	7,466	8,651	10,201	12,329	13,001
90,592	78,585	75,718	61,060	53,771	52,900	56,871	65,479	67,191	62,558	66,333	71,881	73,794	78,511	82,755

At certain colonies, however, man has continuously harvested gannets for his own use, apparently without endangering the population. This is true of no colony in the Gulf of St Lawrence, or in the south-west Britain group; but applies to Ailsa Craig up to about 1880; to the Bass Rock up to 1885; to St Kilda up to 1910; to Sule Stack up to 1932; and to Sula Sgeir, Myggenaes, the Westmann Islands and Eldey up to the present day.

There is no doubt that at the majority of these

every year (and when they do visit it they are sometimes forced to depart prematurely); and there is still a danger that improved methods of transport, or a greater demand for gannet flesh, may materially alter the situation in Lewis or Iceland. In 1940 Eldey was declared a sanctuary, and all gannet-taking stopped there; it will be interesting to see whether the human predation in the Westmann Islands alters as a result of this, with consequent effect on the balance of gannet numbers in this

colony. Mr Malcom Stewart believes that the gannets at Sula Sgeir should be entirely protected, as those elsewhere in Britain, and at Eldey, now are. We are not convinced that absolute protection of this colony is necessary, or indeed desirable in view of the very ancient custom of taking gannets here after a 45-mile journey in an open skeffa from Ness. But

5. OTHER FACTORS AFFECTING THE STATUS OF GANNET COLONIES

A preliminary discussion of points of biological interest shown by the history of gannet colonies has been made by Fisher & Venables (3). We may expand parts of this under the following headings:

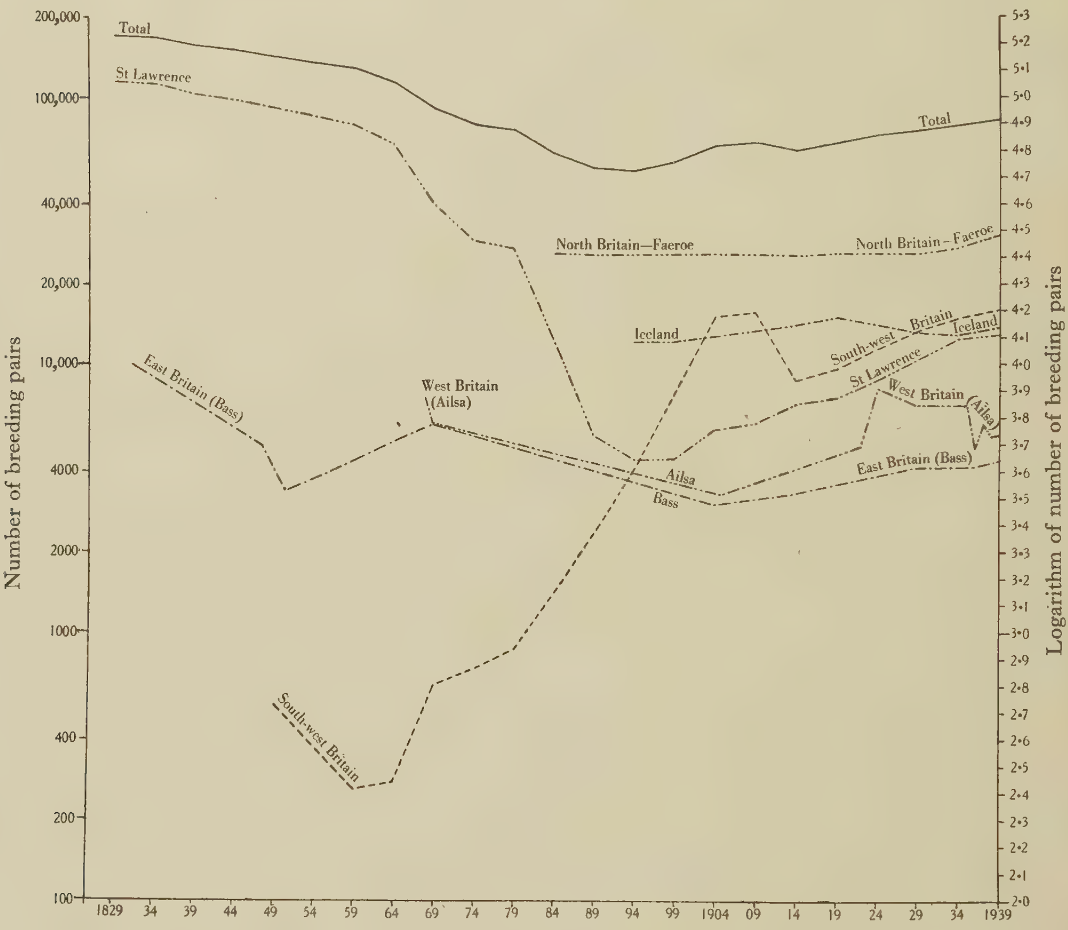

Fig. 4. The population of gannets, by groups, and the world total, 1829–1939.

Ordinate: number of pairs breeding in the groups, and in the world, plotted on logarithmic scale.
Abscissa: years from 1829 to 1939.
The plots of the groups do not begin until the year of, or a year later than, the first reliable count or estimate of a major colony within the group. The plots of west and east Britain are from direct data, the rest from Table 1.

we do suggest that future harvesting be consciously planned and, in view of the recent decline in numbers at this colony, we would propose that no more than a thousand young should be taken in any one year, until further scientific census work justifies an alteration in this number.

(*a*) *Habitat selection.* The limited number of places where the North Atlantic gannet breeds are of a distinct type. Of the 23 stations at which gannets were present in the breeding season of 1939, 19 were on small islands. One (Hermaness) was on stacks lying off, and partly on the mainland of, a

large island (Unst). Three (Bempton Cliffs, Gull-cliff Bay and Cape St Mary) were on steep mainland cliffs. All colonies face large open-sea fishing grounds.

At the colonies gannets always nest either on broad ledges on steep and high cliffs, or on flat or sloping ground on the summits of isolated stacks. These summits are all above high cliffs except at Grassholm and the Scar Rocks. At greatest density on flat or sloping ground each nest occupies about 1 sq.m.

(*b*) *Colonization.* It is quite clear that the colonization of many colonies has continued for long periods from without. In the history we have related, large numbers of the world's gannets have from time to time sought breeding sites at places other than that in which they were hatched. Apart from overcrowding or persecution at the parent colony, we can suggest little about the nature of the pressure which causes them to do so.

It has been suggested by Fraser Darling (1) that once gannets have found a new site which is suitable, a certain minimum, or threshold number of birds may have to be present before the inhabitants of the new colony can breed successfully. We must examine, therefore, the early history of those new colonies about which we have accurate information. These are:

Cases where one, or a few pairs, have been present in the breeding season without success in breeding (5)

2. **Lundy.** In 1922 a single adult gannet attempted to build in May, but left in June.

4. **Great Orme.** In 1941 gannets were seen flying round the cliffs in May, and a pair was seen in occupation of a ledge, and pairing. None was seen after May.

11. **Isle of May.** In 1922 a pair of gannets attempted to nest without success.

12. **Calf of Man.** In 1939 a pair of adult gannets were seen, in the summer, on the south-west cliffs, but were not proved to breed.

24. **Copinsay.** Single pairs were present, without successful breeding, on or about the cliffs here in 1907 or 1908, 1911, and 1925 or 1926.

Cases where a few pairs have been present in the breeding season for some years with only partial success in breeding (2)

7. **Great Saltee.** Either 1, 2 or 3 pairs present 1929–1943. In 1933 single pair reared young. When more than 1 pair present at least 1 egg always produced; failures to breed (or no proof breeding) when 1 pair present, except in 1933.

9. **Bempton Cliffs.** 1–4 pairs present in some years between 1924 and 1942. One pair present 1924–6, 1928, 1929, 1937. In 1937 egg laid. Two pairs reared 1 young 1938; 4 pairs reared 1 young 1939. Birds present in small numbers 1940–2 but exact breeding success not known.

Cases where colonies have been successfully, and fairly rapidly, established (6)

6. **Bull Rock.** Birds first seen on rock 1853; first nests found 1856; 11 pairs 1858. 'Many hundreds' but only few addled eggs and non-breeders present 1868; subsequent history rapid increase.

13. **Scar Rocks.** In 1939, though 2–6 pairs were present, only 1 pair reared young. Pairs present about 10 1941, about 25 1942, about 45 1943; but breeding success not known, though many of the 1942 nests contained young.

25. **Noss.** No birds present in 1909; first showed interest 1911 or 1912; one pair bred 1914; 4 1915; 3 young reared 1918; 5 pairs bred 1919; 10 1920; subsequently increase was rapid. No evidence about breeding success of the few pairs present during early history.

26. **Hermaness.** Not breeding 1913; colony established 1917, no evidence about numbers or breeding success in that year, but at least 109 pairs by 1920.

36. **Gull-cliff Bay.** Possibly present since 1913; breeding in some numbers 1919 or 1920, 1921, 1922, over 100 pairs 1923, but no evidence about numbers or breeding success in early years.

37. **Cape St Mary.** Not breeding in about 1877; 3 pairs 1879; 8–10 pairs 1883; well established by 1890.

38. **Bacalieu Island.** Except that it was established in about 1901, the early history of this colony is quite unknown. There were about 200 pairs in 1941.

39. **Funk Island.** Not breeding, no birds seen, 1934; 7 pairs breeding 1936 out of a total population of about 40 birds.

From the history of these colonies it is at once clear that when small numbers of gannets are present at a colony, breeding is abnormally inefficient. Nevertheless, a lone pair of gannets has bred at a station more than once. It would appear that Fraser Darling's general thesis is correct when applied to the gannet.

We cannot yet expect, with any confidence, that the gannets at Great Saltee and Bempton Cliffs will establish strong colonies. And there is certainly no reason to suppose that the gannets which have been lately seen about the cliffs of the Great Orme and the Calf of Man must necessarily found colonies.

6. SUMMARY

1. The world population of the gannet (*Sula bassana*) was 165,600 ± 9500 in 1939. The methods by which this figure was compiled are discussed in Part 1 of this paper. This part, Part 2, is devoted to a discussion of trends in the gannet's population since 1834.

2. In 1834 the world population was of the order of 334,000 breeding individuals, of which two-thirds (approximately) were breeding on the Bird Rocks in the Gulf of St Lawrence.

3. There was a steady decrease in the world population, mainly owing to the depredations of man at the Bird Rocks, until about 1894, when it was of the order of 106,000 breeding individuals.

4. From 1894 until the present day there was a steady recovery in numbers, and an establishment of new colonies, some now large and successful. This recovery was dominated largely by the remarkable rise of the gannets in south-west Britain.

5. The fall in the numbers of the gannet took place in a period in which man paid no heed to the effects of his unplanned destruction and exploitation of gannets.

6. The rise in the numbers of the gannet has taken place in a period in which man still exploits the gannet; protection has stopped the unplanned destruction which, if continued, would have made an end of the gannet in some parts of its limited range; in the colonies which are still harvested over-exploitation does not persist (though it is suggested that the taking of young birds at Sula Sgeir should be arranged in future under planned limits); and most of the 22 colonies where the gannet is now breeding are entirely protected.

7. There is no indication that the present steady rise in the numbers of the gannet will cease.

8. Gannets have appeared at several new stations in the period under review (1834–1939). Of the 22 present breeding-colonies (which exclude Great Saltee) no less than 9, and probably a tenth and eleventh (Grassholm and Bonaventure) have been established since 1834.

9. When small numbers of gannets are present at a colony, breeding is abnormally inefficient.

REFERENCES

1. **Darling, F. Fraser (1938).** 'Bird flocks and the breeding cycle. A contribution to the study of avian sociality.' Cambridge.
2. **Fisher, J. (1939).** 'Britain's gannet population.' J. Soc. Pres. Faun. Emp., New Ser., Pt. 38: 16–20.
3. **Fisher, J. & Venables, L. S. V. (1938).** 'Gannets (*Sula bassana*) on Noss, Shetland, with an analysis of the rate of increase of this species.' J. Anim. Ecol. 7: 305–13.
4. **Fisher, J. & Vevers, H. G. (1943).** 'The breeding distribution history and population of the North Atlantic gannet (*Sula bassana*) Part 1. A history of the gannet's colonies, and the census in 1939.' J. Anim. Ecol. 12: 173–213.
5. **McWilliam, J. M. (1942).** 'The Scar Rocks gannetry, 1942.' Brit. Birds, 36: 62–4.
6. **Ó Crohan, T. (1943).** 'The islandman.' Harmondsworth, Penguin Books; transl. Robin Flower.

STUDIES ON THE BIOLOGY OF THE EARLY STAGES OF THE SALMON (*SALMO SALAR*)

4. THE SMOLT MIGRATION IN THE THURSO RIVER IN 1938

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(With 3 Figures in the Text)

CONTENTS

1. INTRODUCTION

Previous papers in this series have dealt with the results of studies on the growth and feeding of young salmon carried out between June 1935 and October 1938. Between October 1937 and October 1938 these investigations were made on some tributaries of the Thurso River, and in connexion with this work it was decided to study the smolt migration in the Thurso River in the spring of 1938. The present paper deals with the results obtained.

Numerous investigations have been made in the past on the seaward migration of *Salmo salar* and other related species, but the results obtained have been limited in nearly every case by the fact that observations were made at only one point on the river concerned. Since it appeared that results of greater value could be obtained by studying the movement, growth and development of the smolts simultaneously at a number of points on the same river, it was decided to construct traps at several different points on the Thurso River, and to study the movements of the smolts past these points.

The Thurso River, which has a length of about 62 km., lies in Caithness in north-eastern Scotland, and flows in a northerly direction to enter the sea in Thurso Bay. The nature of the river and the surrounding country has been described in a previous paper (Allen, 1941). The course of the river and its principal tributaries, together with the positions of the traps, are shown in Fig. 1.

2. METHODS AND APPARATUS

Four traps were constructed, two between the sea and Loch More, and two above Loch More. The locations of these were:

(*a*) *The Halkirk Trap*. Situated about 200 m. below the railway bridge, about 14·8 km. from the sea.

(*b*) *The Loch Beg Trap*. Situated about 0·5 km. below Loch Beg, and 22 km. above the Halkirk Trap.

(*c*) *The Dalnaha Trap*. Situated about 400 m. above Loch More and 4 km. from the Loch Beg Trap.

(*d*) *The Dalganachan Trap*. Situated about 100 m. above the junction of the Rumsdale Water and 8·5 km. above the Dalnaha Trap.

The plan of a typical trap is shown in Fig. 2, and although individual traps varied in their proportions in order to adapt them to local conditions all four were of this type. The main and subsidiary leaders, *AB* and *DE*, and the pound *BGFDC* were made of wire netting of ½ in. (1·3 cm.) mesh, supported by heavy netting of approximately 6 in. (15 cm.) mesh, and carried on wooden posts. The netting was 4 ft. (1·2 m.) wide and the lower edge was well buried in the bed of the river and anchored with hooked iron pegs. The pound, which measured approximately 2 × 1·5 m., and the subsidiary leader were rigidly constructed, the posts being firmly driven into the river bed and also supported by guys. The entrance into the pound of each trap was formed by a funnel of wire netting, about 40 cm. long and tapered from 10 to 6 cm. in diameter, leading inwards from the angle *C*.

Since it was not possible in the time available to build traps strong enough to withstand a really heavy flood, it was considered desirable to build the traps in such a way that while they might collapse in a big flood they could be quickly and easily repaired afterwards. For this reason the main leader of all the traps except that at Dalganachan was not constructed rigidly, like the pounds and subsidiary

Fig. 1. The course of the Thurso River, showing the positions of the traps, the principal tributaries and the places referred to in the text.

leaders, but was firmly anchored at the bottom and was supported by posts which merely rested on the river bed, held upright by props and light guys. It was hoped that in a heavy flood the props would be displaced and the guys broken, so that the leader would lie flat, allowing the water to pass over it. Since it was not actually displaced the leader could be easily cleaned and restored to its fishing position after the flood had passed. The advantage of this type of construction was shown by the floods on 23 May and subsequent days which seriously damaged and finally destroyed the Dalganachan Trap but did only minor damage to the others. In the Halkirk and Loch Beg Traps a gap about 2 m. wide had to be left between the upstream end of the main leader and the bank so as to allow the passage of adult salmon upstream.

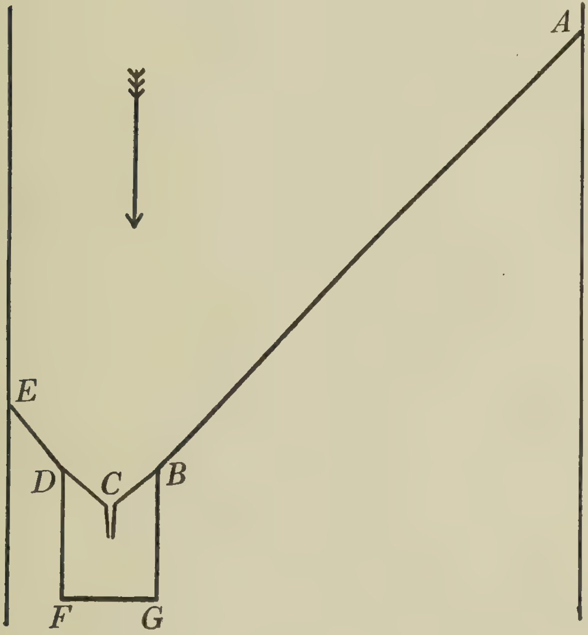

Fig. 2. The plan of a typical trap.

In addition to the four traps described above a stop-net was maintained in the Sleach Water just above its outflow into Loch More, about 2·5 km. above the Loch Beg Trap. This was a net of ½ in. (1·3 cm.) knot-to-knot netting, with a length about twice the width of the stream. This net was set across the Sleach Water with one end as far as possible above the other, and was usually drawn daily. The upstream end was first pulled rapidly across to the opposite bank so as to enclose any fish lying close to the net, which was then drawn on shore. After the removal of the fish the net was reset as quickly as possible.

The four fixed traps were completed on the following dates: Dalganachan, 16 April; Dalnaha, 20 April; Loch Beg, 2 May; Halkirk, 8 May. After completion the traps operated continuously until 23 May, when a moderate flood occurred. This flood detached from the river bed large quantities of filamentous algae, which were carried down and completely blocked the netting of the traps above Loch More so that the main leaders of both collapsed. The trap at Dalganachan was repaired on 25 May, and that at Dalnaha on 26 May, although a further small flood on 27 May caused further damage to both traps, which was repaired the following day. On 29 May, however, another moderate flood occurred, which completely wrecked the Dalganachan Trap. As it appeared probable that most, if not all, of the smolts had left the upper river by this time, no attempt was made to rebuild this trap. The Dalnaha Trap sustained slight damage, but was repaired and continued in operation for a further week. It was then removed, as the smolt run here appeared to be over.

Owing to the stabilizing effect of Loch More, the outlet of which is controlled by sluices, the rise in the river below this was considerably less, both in extent and suddenness, and consequently the floods did no serious damage to the two lower traps. These two traps operated continuously until 10 June when they were removed as the smolt run appeared to be virtually over. The stop-net in the Sleach Water was first set on 25 April and was finally removed on 20 May, as no smolts had been caught in it for more than two weeks.

All the traps were visited either daily or every other day, and at each visit the smolts which had been caught were removed from the pound, counted and liberated below the trap. Except on a few occasions when unusually large numbers were caught, each smolt was weighed, its length measured, a sample of scales taken, and the degree of smolt development recorded. Weights were determined by means of a spring balance, to the nearest 0·5 g.; lengths were measured from the snout to the fork of the tail, to the nearest 0·1 cm.; and scale samples were taken from the area between the anterior end of the dorsal fin and the lateral line. The determination of the degree of smolt development was based on the colour of the pectoral fins. Except on a few occasions each smolt was marked before being liberated, sometimes by attaching a numbered silver tag to the dorsal fin, but usually by clipping off portions of fins. It was considered practicable to mark the fish by removing only the distal third of the fins concerned, since any recaptures would occur fairly soon after marking, and regeneration would not proceed to any great extent. Also, this degree of fin-clipping appeared to be unlikely seriously to affect the fish. Eight separate fin-clips were used: on the adipose fin, the dorsal and ventral lobes of the tail, the anal fin, the left and right pelvic fins, and the left and right pectoral fins. The use of these,

singly and in combinations of two, three and four, allowed 162 distinct markings to be made, and it was therefore possible to apply a distinctive mark to all the fish liberated from each trap on each day.

3. RATE OF CATCH AND RATE OF TRAVEL

There are two ways in which data regarding the nature of the smolt migration and the factors affecting it can be obtained from the results of the trapping. These are by studying the fluctuations in the number of smolts caught in each trap during successive periods, and by observing the movements from trap to trap of marked smolts. An ideal trap would retain all fish attempting to pass downstream, and would exercise no check on the downstream movement, so that all fish which would normally have passed the site of the trap would be caught. In practice it is probably rare to achieve such ideal results, and in the present instance it was impossible in the case of the two lower traps, since in these it was necessary to leave small gaps in the leaders. As will be shown later, the majority of smolts reaching these points passed through the gaps instead of entering the trap itself. At Halkirk, probably as the result of the pound being placed in a side channel with a comparatively slight current, the efficiency of the trap was extremely low, and it is unlikely that the rate of catch here provides any indication of the activity of migration. At Loch Beg, where the pound was situated in the main stream, the efficiency was considerably higher, about 17·5 %, and probably the fluctuations in the rate of catch here do reflect fluctuations in the actual intensity of the migration. In the upper traps where no gap was left it is probable that all smolts attempting to pass downstream were captured, except during periods when the traps had been damaged by floods. A few exceptionally small smolts were also observed to pass through the netting. Since, however, smolts travelling downstream may have delayed before passing through the narrow opening into the trap, it is possible that the rate of catch, even in the two higher traps, does not reflect exactly the activity of migration.

At Dalganachan considerable numbers of smolts were observed to accumulate in a pool a short distance above the trap, and very few smolts were taken in this trap until 23 May. On this day considerable numbers entered it during the early stages of the flood. These facts suggest that this trap had a very considerable checking effect, and that its catches were therefore not truly indicative of the actual activity of migration. At Dalnaha shoals of smolts were frequently observed in a pool immediately above the trap, but the numbers were not great compared with those that actually entered it on many occasions, and it is therefore probable that here the checking action was slight, and that the rate of catch reflects the activity of migration to a considerable extent. Thus it appears that only at Dalnaha and Loch Beg does the rate of catch provide an indication of the actual activity of the smolt run, and is thus of value in attempting to elucidate the causes of fluctuations in this activity.

Table 1 shows for each of the traps the number of smolts caught during the periods between each visit, and the average number caught per hour, and in Fig. 3 the rates of catch at Dalnaha and Loch Beg are shown graphically. Table 1 shows also the water level at these traps on each occasion when they were visited. The levels were measured on posts placed in the stream a short distance below each trap. As it was impossible to visit any trap at the same time each day, no satisfactory results could be obtained by recording the temperature of the water at the traps. Daily temperature readings were, however, taken at 9 a.m. in the Sleach Water at Altnabreac, and in the Sinclair Burn just above its confluence with the Thurso River. These temperatures probably provide a fair indication of the fluctuations at the traps, although those at Loch Beg were probably somewhat damped by Loch More. The daily temperatures at Altnabreac and the Sinclair Burn are shown in Table 1, and those for the Sinclair Burn are included in Fig. 3, together with the water levels at Dalnaha and Loch Beg.

When day-to-day fluctuations are neglected, the rate of catch at Loch Beg shows certain definite trends, which appear clearly in Fig. 3. At the commencement of observations the rate of catch was high, but it declined steadily until about 16 May. From then until 20 May practically no smolts were caught, but on that date the catch began again to increase, and this increase continued and culminated in the large catch of 25 May. After 25 May the catch declined rapidly almost to zero. This decline was probably due to the fact that practically all the smolts had then left that part of the river. Probably, however, the earlier fluctuations in the catch were largely the result of variations in the activity of the smolts. The agreement between the fluctuations in the rate of catch at Loch Beg and the rate of travel of marked smolts between Dalnaha and Loch Beg, as shown in Table 2, supports this hypothesis. If this view is correct smolt activity was declining during the period 3–16 May, was practically zero from 16 to 19 May, and increased from 20 to 25 May. Table 2 shows that the smolts marked at Dalnaha between 2 and 7 May arrived steadily at Loch Beg from the time of the completion of the trap until 14 May. From then until 20 May none were taken, but from this date onwards they again arrived steadily. It also appears that the rate at which the migrating smolts were travelling was decreasing during the period in which the rate of catch declined. The average time taken to travel from Dalnaha to

Table 1. *The number of smolts caught and the rate of catch (smolts per hour) for each day, together with comparable water levels and temperatures*

	Sleach Water		Dalganachan			Dalnaha			Loch Beg			Halkirk		Temp. (°C.)	
Date	No. of smolts	Rate of catch	No. of smolts	Rate of catch	Water level in.	No. of smolts	Rate of catch	Water level in.	No. of smolts	Rate of catch	Water level in.	No. of smolts	Rate of catch	Sinclair Burn	Sleach Water
20 April	.	.	1	0.02	5.5	.	.	.	.	.	.	.	.	6.0	8.75
21	.	.	0	0	5.5	1	0.05	1.5	.	.	.	.	.	6.0	9.0
22	.	.	0	0	5.0	13	0.81	1.5	.	.	.	.	.	7.5	8.75
23	.	.	0	0	.	20	0.76	1.5	.	.	.	.	.	8.5	9.75
24	.	.	0	0	5.5	7	0.28	1.0	.	.	.	.	.	10.5	10.0
25	.	.	0	0	5.5	11	0.46	1.0	.	.	.	.	.	11.0	7.5
26	.	.	A	A	A	A	A	A	.	.	.	.	.	10.0	9.5
27	.	.	0	0	5.0	57	1.05	1.0	.	.	.	.	.	9.0	10.75
28	5	0.08	0	0	5.0	29	1.61	1.0	.	.	.	.	.	7.0	8.5
29	30	1.28	0	0	5.0	7	0.29	1.0	.	.	.	.	.	7.0	7.75
30	42	1.77	0	0	5.0	4	0.15	0.5	.	.	.	.	.	9.5	8.0
1 May	0	0	1	0.05	.	2	0.10	0.5	.	.	.	.	.	11.0	11.0
2	20	0.71	1	0.04	.	59	2.11	0.5	.	.	10.0	.	.	11.5	11.25
3	A	A	A	A	A	A	A	A	165	5.07	14.0	.	.	12.5	12.0
4	10	0.22	1	0.02	4.5	47	1.03	0.5	107	4.64	13.0	.	.	14.0	12.0
5	1	0.03	A	A	A	49	1.71	0.5	39	1.84	12.5	.	.	14.5	11.75
6	A	A	A	A	A	A	A	A	A	A	A	.	.	11.0	9.0
7	1	0.02	1	0.01	5.0	20	0.45	0.5	122	4.00	11.5	.	.	9.0	8.0
8	0	0	A	A	A	1	0.03	1.0	40	1.78	11.2	0	0	8.5	7.5
9	A	A	A	A	A	A	A	A	A	A	A	A	A	8.5	7.0
10	0	0	0	0	5.0	8	0.17	0.5	25	0.49	11.0	0	0	11.5	7.5
11	A	A	0	0	5.0	3	0.12	1.0	13	0.84	11.0	17	0.74	11.0	8.5
12	0	0	0	0	5.0	30	1.32	1.0	13	0.53	10.5	2	0.09	10.5	12.25
13	0	0	A	A	A	39	1.59	1.0	31	1.02	10.5	A	A	9.0	12.0
14	B	B	0	0	5.5	13	0.51	1.0	15	0.56	10.5	23	0.46	8.5	12.5
15	0	0	0	0	5.7	A	A	2.0	11	0.61	10.5	7	0.28	8.0	13.0
16	0	0	0	0	5.5	45	1.00	1.7	1	0.03	10.5	1	0.05	8.0	11.0
17	A	A	A	A	A	A	A	A	A	A	A	A	A	9.0	11.0
18	A	A	1	0.02	5.0	36	0.73	1.0	0	0	10.5	26	0.55	10.5	9.25
19	A	A	A	A	A	A	A	A	A	A	A	A	A	9.0	8.0
20	0	0	0	0	5.0	21	0.42	1.0	11	0.22	10.5	3	0.06	11.5	11.5
21	.	.	1	0.04	5.0	42	1.77	1.0	16	0.51	10.0	1	0.04	10.5	11.5
22	.	.	0	0	5.0	13	0.54	0.5	18	1.09	10.0	60	2.31	.	14.0
23	.	.	26+	1.04+	11.5	7	0.28	11.0	5	0.24	10.0	16	0.87	.	10.0
24	.	.	B	B	13.5	B	B	14.0	40	1.27	14.0	8	0.29	.	9.0
25	.	.	B	B	7.0	B	B	.	107	6.31	14.0	23	0.85	.	7.75
26	.	.	0	0	6.2	B	B	3.5	36	1.15	14.0	13	0.68	.	10.0
27	.	.	B	B	12.0	0	0	12.0	22	1.37	14.0	2	0.07	.	10.25
28	.	.	0	0	6.5	0	0	.	A	A	.	A	A	.	10.0
29	.	.	B	B	.	B	B	.	39	0.81	.	13	0.27	.	8.5
30	.	.	.	.	.	B	B	.	9	0.38	.	0	0	.	10.0
31	.	.	.	.	.	0	0	.	11	0.46	.	7	0.29	.	10.0
1 June	.	.	.	.	.	0	0	.	9	0.38	.	0	0	.	10.5
2	.	.	.	.	.	0	0	.	1	0.04	.	0	0	.	10.0
3	.	.	.	.	.	0	0	.	1	0.04	.	1	0.04	.	10.5
4	.	.	.	.	.	.	.	.	5	0.21	.	2	0.08	.	12.5
5	.	.	.	.	.	.	.	.	1	0.04	.	0	0	.	12.0
6	.	.	.	.	.	.	.	.	0	0	.	1	0.04	.	12.5
7	.	.	.	.	.	.	.	.	1	0.04	.	0	0	.	13.0
8	.	.	.	.	.	.	.	.	0	0	.	2	0.08	.	13.75
9	.	.	.	.	.	.	.	.	A	A	.	A	A	.	13.0
10	.	.	.	.	.	.	.	.	1	0.02	.	1	0.02	.	14.0

A denotes trap not visited. B denotes trap not operating.

Loch Beg increased steadily from the commencement of observations at Loch Beg till the apparent cessation of activity on 16 May. For the three batches of smolts which left Dalnaha on 2, 4 and 5 May the average times taken to reach Loch Beg by those smolts which arrived there before 16 May were 4.7, 5.7 and 6.0 days. These results are thus in agreement with the hypothesis that smolt activity was declining up to about 15 May, and was then almost zero until it recommenced on 20 May.

The hypothesis that the smolts in the section of the river above Loch Beg recommenced active migration before 20 May is also supported by the data obtained from the recapture of marked smolts. The majority of smolts which left Dalnaha on and after 11 May reached Loch Beg during or soon after

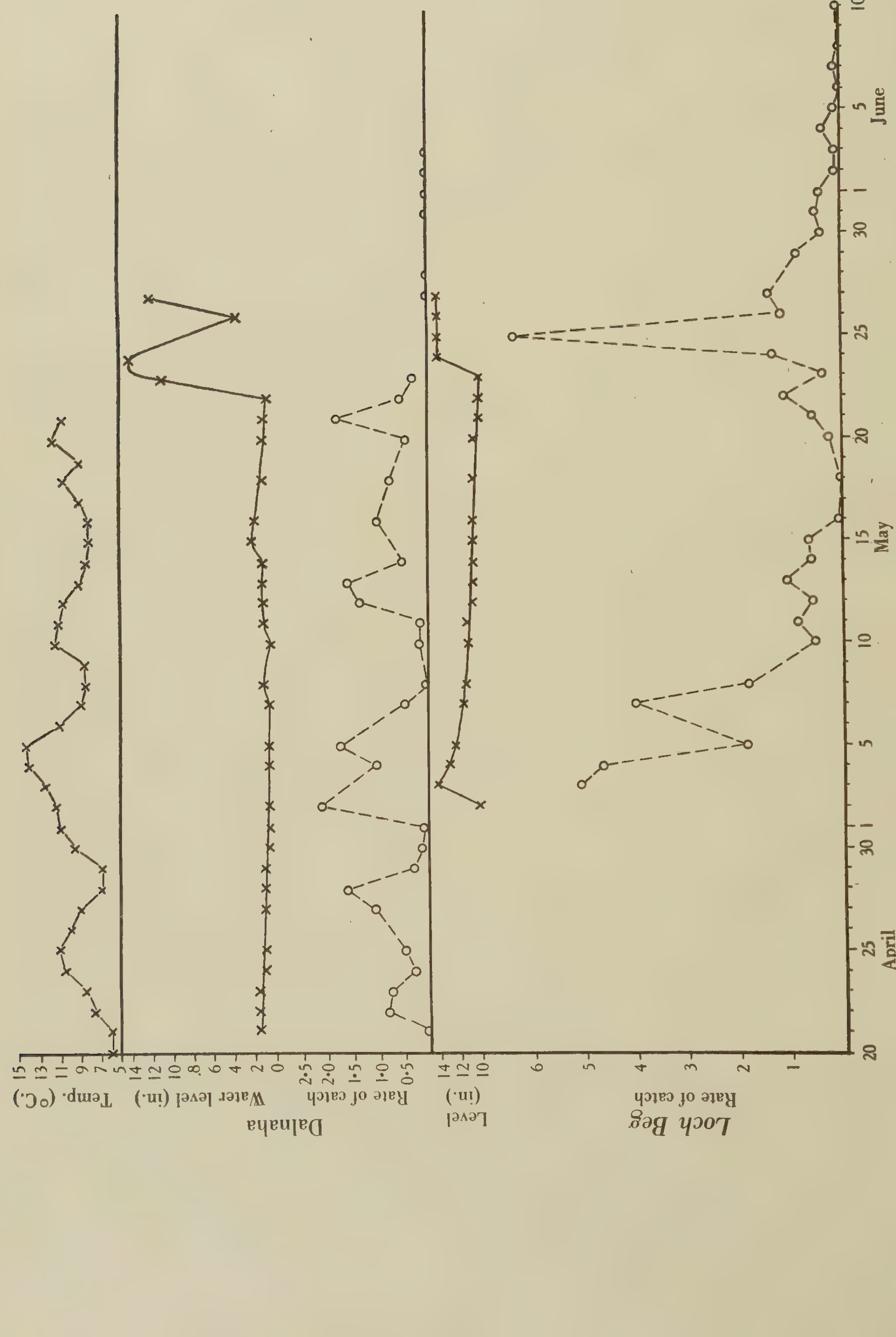

Fig. 3. The daily fluctuations in the water-level and rate of catch (smolts per hour) at Dalnaha and Loch Beg, and in the temperature of the Sinclair Burn.

the peak catch of 24 and 25 May, but a few arrived there considerably earlier. These latter fish took approximately the same time over the journey as that taken by fish during the early part of the first period of activity. The very high rate of catch recorded at Loch Beg on 24 May and particularly on 25 May suggests that the activity of migration reached a very high level in this section of the river at that time. This view is supported by the study of the origin of the smolts recaptured at Loch Beg on these days. Tables 2 and 3 show that on these days smolts were caught which had left Dalnaha and the Sleach Water over a long preceding period. A large proportion of those recaptured on 25 May had, however, left Dalnaha only 3–5 days before. These results support the hypothesis that a high degree of activity occurred at this time. Further evidence of the high rate at which smolts were travelling is given by the fact that, as shown in Table 4, the catch at Loch Beg on 25 May and the succeeding days included a number of smolts which had been marked at Dalganachan and were still above Dalnaha when the trap there collapsed.

Similar results regarding the movements of the smolts in the Loch More area were obtained from the capture at Loch Beg of smolts marked in the Sleach Water, as shown in Table 3. The smolts which were marked in the Sleach Water between 29 April and 2 May arrived at Loch Beg in steadily decreasing numbers from the completion of this trap until 15 May. Thereafter none were taken until 22 May, but between 22 and 26 May seven were caught. Thus it appears that the activity of smolts migrating through the Loch More area from the Sleach Water showed similar fluctuations to that of smolts originating in the upper part of the Thurso River.

The fluctuations in the catch at Dalnaha do not show such distinct trends as at Loch Beg, and there was not in this case a distinct early period of steadily decreasing catch. There was, however, a period, from 8 to 11 May, when the rate of catch was very much less than in the preceding weeks, and after this time the rate of catch increased rapidly and subsequently oscillated about a fairly high mean. It appears probable that this period of low rate of catch represents a period of low activity, and that the following period of high rate of catch resulted from the resumption of active migration. Data regarding the activity of smolts in the section of the river above the Dalnaha trap are also provided by study of the movement of marked fish between Dalganachan and Dalnaha as shown in Table 4. It will be seen that these results support the conclusion reached from the examination of the rate of catch at Dalnaha. The smolts leaving Dalganachan between 20 April and 4 May took progressively longer times to reach Dalnaha, while those which left Dalganachan on 7 and 18 May had not reached Dalnaha when the flood temporarily washed out the trap there on 23 May. On the other hand, the smolt which was marked at Dalganachan on 20 May reached Dalnaha before the flood. These data not only support the conclusions reached from the study of variations in the rate of catch, but also suggest that activity was decreasing during the early part of the observations. The fact that the latter effect was not shown by the rate of catch may have been due to an increase during this period in the number of smolts present in the area.

Since the main leader of the Dalnaha Trap collapsed a few minutes after the water began to rise there in the flood of 23 May, the records of this trap do not show whether there was any increase in activity here associated with this flood. However, when the trap was repaired no further smolts were caught, although the frequent capture of brown trout showed that the trap was working satisfactorily. This suggests that migration in this section was so active during the period when the trap was not operating that it removed all smolts from this section of the river. On the other hand, the Dalganachan records do show that there was a great increase in activity associated with the flood of 23 May. Table 1 shows that prior to this day very few smolts entered this trap, although they were observed to accumulate in a pool above it. A number of these smolts were netted on 21 May and marked and liberated below the trap. On 23 May, however, 26 smolts were removed from the trap in the short period before the river overflowed it, and there appeared that there were at least as many more which could not be removed in time. Of these 26 smolts six (23 %) arrived at Loch Beg either in the peak catch of 25 May or on the following day. Since Table 2 shows that the average efficiency of this trap was about 18 %, it appears probable that practically all the smolts passed Loch Beg on these days.

As has already been pointed out, no satisfactory results can be obtained from studying fluctuations in the daily catch at Halkirk, and insufficient smolts were recaptured there to provide much data regarding fluctuations in activity in the section of the river above this trap. The few recaptures which were made do, however, show that smolts marked at Loch Beg between 3 and 15 May arrived at Halkirk after 14–25 days, while smolts marked on 25 and 26 May reached Halkirk after 5 or 6 days. This suggests that in this section of the river also the activity of migration of the smolts which passed Loch Beg in the peak about 25 May was considerably greater than that of the smolts migrating earlier.

Thus it appears that the trends in the activity of migration were similar, at least in the two sections of the river above Loch Beg and above Dalnaha. In each case a period of decreasing activity terminated in a short period during which activity was practically nil. This was followed by a further period

Table 2. *The number of smolts arriving each* … Date of …

Date of departure	No. marked	May 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
22 April	13	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
23	21	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
24	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
26	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	47	6	.	3	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
28	29	1	3	1	.	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.
29	7	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
30	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1 May	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	57	.	3	1	.	2	.	.	1	.	.	1	.	.	.	.	.	.	.	.
3	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	44	.	.	.	.	4	.	.	2	.	1	1	1	.	.	.	.	.	2	.
5	49	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	1	1
6	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	20	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
8	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
15	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16	45	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1
17	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	36	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
19	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
20	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
21	37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
22	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
23	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Totals	563	9	7	5	.	8	1	.	5	.	2	3	1	1	.	.	.	.	5	3

Table 3. *The number of smolts arriving each day at* … Date of …

Date of departure	No. marked	May 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
28 April	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
29	30	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.
30	42	.	3	1	.	3	.	.	.	.	1	.	.	.	.	.
1 May	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	18	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
3	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	9	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Totals	106	3	4	1	.	3	1	.	.	.	1	.	.	1	.	.

day at Loch Beg, having been marked at Dalnaha

arrival

May										June											
22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	Total arrivals	Percentage arrivals
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	8
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	23
1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	35
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	14
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	9	16
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	25
1	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	16
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2	10
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	33
.	.	2	2	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	7	23
.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	5
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	9
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	2	1	2	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	7	20
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	4	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	9	45
.	.	.	5	1	1	.	1	1	1	.	.	.	.	.	.	.	.	.	1	11	30
.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	4	31
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
3	.	7	19	5	2	.	8	1	2	.	.	.	.	.	.	1	.	.	1	99	17·6

Loch Beg, having been marked in the Sleach Water

arrival

May														June			
18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	Total arrivals	Percentage arrivals
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	6	20
.	.	.	.	.	.	1	2	1	.	.	.	.	.	.	.	12	29
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	6
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	22
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.
	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	100
.	.	.	.	1	1	2	2	1	.	.	.	.	.	1	.	22	20·8

of active migration, culminating in a wave of very vigorous activity in which the great majority of smolts left at least the upper part of the river. Certain deductions may be made as to the causes of these fluctuations. If they were due to variations in meteorological conditions or any other environmental factors which affected the area as a whole, corresponding events would occur simultaneously in the two sections. But, except in the case of the final phase of very vigorous activity, the events in the area above Dalnaha preceded their counterparts in the Loch Beg section by about 8 days. Therefore it does not appear likely that meteorological or other general conditions caused the other major changes in smolt activity. The time lag between events at Dalnaha and Loch Beg would, however, arise if the fluctuations in activity of migration took the form of waves travelling down the river. Such waves might be either waves of smolts or else waves of activity.

smolts marked at Dalnaha on 4 and 5 May eleven were recaptured at Loch Beg during the first period of activity between 7 and 14 May, and were evenly distributed over this period. No more were recaptured at Loch Beg until 20 May, and then between 20 and 25 May eight were recaptured during the second period of activity, being again evenly distributed over the period. Thus, of the smolts which left Dalnaha during the first period of activity only about half reached Loch Beg during the corresponding phase, while the remainder did not reach this trap until the next period of activity. These results again illustrate the extent to which the smolts become scattered on their way downstream, and show that waves of migrating smolts do not occur to any great extent.

It therefore appears possible that the fluctuations in catch may be due to waves of activity. Such waves must result from the travelling down the river of a

Table 4. *The arrival at Dalnaha and Loch Beg of smolts marked at Dalganachan*

		Dalnaha							Loch Beg					
		Date of arrival							Date of arrival					
Date of departure	No. marked	April 23	May 12	May 13	May 17	May 23	Total arrivals	Percentage arrivals	May 25	May 26	May 29	May 30	Total arrivals	Percentage arrivals
20 April	1	1	.	.	.	.	1	100	.	.	.	.	0	0
1 May	1	.	1	.	.	.	1	100	.	.	.	.	0	0
2 May	1	.	.	1	.	.	1	100	.	.	.	.	0	0
4 May	1	.	.	.	1	.	1	100	.	.	.	.	0	0
7 May	1	.	.	.	.	.	0	0	1	.	.	.	1	100
18 May	1	.	.	.	.	.	0	0	1	.	.	.	1	100
20 May	2	.	.	.	.	1	1	50	.	.	.	.	0	0
21 May	23	.	.	.	.	.	0	0	1	1	.	.	2	9
23 May	26	.	.	.	.	.	0	0	1	1	3	1	6	23
Totals	57	1	1	1	1	1	5	8·8	4	2	3	1	10	17·5

The data about the movement of marked smolts between Dalnaha and Loch Beg appear definitely to discount the possibility of the former alternative. If waves of smolts occurred it would be found that smolts liberated at one trap at one time tended to arrive in a body at the next trap. Table 2 shows that a great scattering in time occurs among smolts leaving Dalnaha on any one day. Nine cases occurred in which seven or more smolts which had been marked at Dalnaha on the same day were recaptured at Loch Beg, and the average interval between the arrival of the first and last smolts in these batches was 13·8 days. Similarly, on 6 days seven or more smolts marked at Dalnaha were recaptured at Loch Beg, and the average interval between the marking of the first and last of these at Dalnaha was 14·2 days. This indicates clearly the great extent to which smolts scatter on their way downstream.

In addition, if waves of smolts occurred, all the smolts which left any one trap during any one phase of the cycle of activity would arrive at the next trap during the corresponding phase. However, of the

stimulus to active migration. If, as appears possible, there is great variation between individual smolts in the degree to which they have developed their migratory reactions, then such a travelling stimulus would not produce equally active migration in all smolts, and would therefore not produce waves of smolts. But it would cause a wave of generally increased activity to travel downstream with it. There are comparatively few possible stimuli which could travel progressively down a river and produce the effects postulated above. Various meteorological effects, such as temperature, light, and general weather conditions, have been suggested as affecting smolt migration, but while they may do so, none of these is likely to show any tendency for changes to travel progressively downstream. Their influence on daily fluctuations in activity will be discussed later.

Rises in water level have, however, repeatedly been shown to affect smolt migration. Thus Berry (1931) found that the main smolt run in the River Tay commenced when a considerable rise in water level occurred, and (1933) also observed that the main run of smolts left the River Ness in a spate.

Bull (1930, 1931) and White & Huntsman (1938) found that the smolt migration appeared to be stimulated by a fall of rain, particularly when this resulted in a rise in stream level. White (1940) records instances of major runs occurring after rainfall or rises in stream level. On the other hand, Berry (1931) and White (1940) found that major runs passed observation points during times of low water level.

Rises in water level usually occur first in the headwaters of a river and travel progressively downstream, and could therefore produce a stimulus of the necessary type. It appears probable that the flood of 23 May produced such an effect. The records for Dalganachan and Loch Beg show that in each case abnormally high rates of catch were recorded on the day on which the rise in level occurred. In the latter case the average rate of catch for the day was actually higher on the second day of the flood, but the average rate of catch recorded on 24 May was based partly on the period before the rise in level occurred, and only partly on the period after it. Further support for the view that water level plays an important part in determining the activity of migration is provided by the fact that the early period of declining activity in both the Loch Beg and Dalnaha areas was also a period of declining water level. It is noticeable that after 7 May, when the minimum rate of catch was recorded at Dalnaha, successive small rises occurred in the water level in this area, and during this time the activity of smolt migration there was increasing. On the other hand, the water level at Loch Beg continued to decline not only during the period of declining and zero activity which continued until 19 May, but also through the period of activity which occurred from 20 May onward. It is therefore evident that a further explanation must be sought for the active smolt migration which occurred in the Loch Beg area from 20 to 23 May.

Comparison of Tables 1 and 2 shows that of the 50 smolts captured at Loch Beg from 20 to 23 May, six were marked at Dalnaha before 7 May during the first period of activity, one on 11 May during the period of inactivity, and only four during the second period of activity. It is therefore clear that the increased activity recorded at Loch Beg during the period 20–23 May did not arise entirely from the movement down to this point of the actively migrating smolts which passed Dalnaha during the second period of activity from 12 May onward. The small rises in water level which stimulated the more active migration of 12 May in the section of the river above Dalnaha occurred also in the short section of the river between Dalnaha and Loch More, and probably also in the other two tributaries of Loch More, the Sleach Water and the Backlass Burn.

It is probable, however, that the total number of smolts remaining in these three areas at this time was very small compared with the total number remaining in the Loch More area, especially since the smolt migration was apparently completed earlier in the Sleach Water than in the main river. It is unlikely therefore that these areas contributed greatly to the increased numbers of smolts taken at Loch Beg during the period 20–23 May. Consequently this increase must have arisen principally from an increase in activity of the smolts already in Loch More and in the section of the river between it and the Loch Beg Trap. No appreciable rise in water level occurred in this area between the commencement of observations and the flood of 23–24 May, and some other stimulus must therefore have produced the increase in activity. It is possible but, considering the smallness of the rises, unlikely that these produced sufficient chemical changes in the water of Loch More and the river below it to stimulate more active migration. This hypothesis is rendered still more unlikely by the fact that these rises occurred at intervals from 8 May onwards, with the largest on 15 May, while activity did not recommence until 20 May. It is therefore necessary to seek another stimulus which will show the required wave effect and will provide an explanation of the phenomena.

It is possible that under certain circumstances the passing of actively migrating smolts would act as a stimulus to other smolts, a possibility that is rendered more likely by the gregarious habit of migrating smolts, since there would be a tendency for a smolt migrating slowly or on the threshold of active migration to be absorbed into and to travel with an actively migrating shoal which moved past it. Such an effect would provide the simplest explanation of the phenomena discussed above. The smolts from the waters above Loch More which had been stimulated to active migration by the freshes migrated through the Loch and down the river past the Loch Beg Trap. Their passage would stimulate to activity a proportion of the smolts in the waters through which they passed, and they would in consequence arrive at Loch Beg in association with a number of smolts from the lower waters in which the original stimulus had not occurred. It therefore appears that the main trends in the activity of the smolt migration in the upper part of the Thurso River in 1938 can be accounted for if the principal stimuli to active migration are rises in water level, and the passage of other actively migrating smolts.

Since the rate of travel, even of actively migrating smolts, is considerably less than that of a rise in water level, smolts which have been stimulated to active migration in this way, will gradually drop further behind the rise. Consequently as a rise in level travels downstream the period of active migration associated with it will gradually increase in duration. This lagging of stimulated smolts behind the stimulus as it travels downstream is well illu-

strated by events associated with the flood of 23–24 May. Twenty-six smolts were marked at Dalganachan on 23 May when moving with the first rise in level; of these six were recaptured at Loch Beg between 25 and 30 May, being then 1–6 days behind the rise. Of the smolts which were marked at Dalganachan on 7, 18 and 21 May, and which were still above Dalnaha when the flood occurred, those which were recaptured at Loch Beg were taken on 25 and 26 May, 1 and 2 days respectively after the rise. At Halkirk, one of the smolts marked at Dalganachan on 21 May was recaptured on 31 May, together with two marked at Loch Beg on 25 and 26 May. Thus the smolts which started active migration in the upper river when the rise in level occurred there were about 7 days behind this rise by the time they reached Halkirk.

In this instance the smolts concerned appeared to be still migrating actively when they reached Halkirk, and it should be noted that the main flood of 23 May was followed, at any rate in the upper river, by a series of smaller freshes. It is probable, however, that where an isolated fresh occurs the distance downstream which the stimulated smolts travel may be limited, since, as they lag behind the rise, they will gradually pass into low-water conditions where they are no longer stimulated to migrate, and as the original impulse to active migration dies down they will probably cease to travel. In many cases the smolts may reach the sea before this occurs. Where, however, the original distance from the sea is sufficiently great, an isolated rise in water level might result in the smolts migrating a certain distance down the river, and then ceasing to travel until again stimulated.

The great divergences in rate of travel shown by individual smolts under similar conditions suggest that different individuals react differently to stimuli towards migration. It appears probable that, like the development of the typical physical characteristics, the tendency to migrate is only developed gradually, and that the process is actually the development of a susceptibility to migration-producing stimuli. Thus a slightly developed smolt will probably not migrate except in response to a violent stimulus, and will then travel only comparatively slowly, while a fully developed will migrate vigorously in response to quite a feeble stimulus.

The number of smolts passing a given point during any period depends on the density of smolts in that area, and on the rate at which they are travelling. The density of the smolts depends upon the quantity originating in the higher parts of the water system, and upon the various conditions which have stimulated them to migrate and so brought them into the area concerned. As has been shown above, individual smolts in similar conditions travel at greatly different rates, and hence the number of smolts passing a given point on one day cannot be regarded as being only the result of the conditions prevailing at the point of observation at that time. It is, however, probably the sum in various proportions of the effects of conditions prevailing at different preceding times and in different parts of the river system. Thus it is probable that, except on occasions of unusual activity, such as those caused by floods, little information can be obtained by studying conditions, and particularly day-to-day fluctuations, at one point only. But where the trap is of such a nature as seriously to impede the migration of smolts, it is possible that it may yield results which reflect to some extent the day-to-day variations in the activity of migration at that point, since the activity with which the smolts are migrating may affect their readiness to enter the trap.

Consideration of the fluctuations in the rate of catch at the various traps does, however, provide some data on the possible influence of various environmental factors on the activity of migration. The only environmental factors which show irregular daily fluctuations similar to those shown by the rate of catch of the traps are those of meteorological origin. Among these factors three types may be considered:

(*a*) Rainfall, and variations in water level.

(*b*) Temperature.

(*c*) General weather conditions including light intensity.

(*a*) *Rainfall and water level.* The influence of water level on the Thurso smolt migration of 1938 has already been discussed and found to be of great importance. The data do not enable any differentiation to be made between rainfall and rises in water level.

(*b*) *Temperature.* The results of previous investigations have yielded somewhat contradictory results regarding the influence of temperature on smolt migration. White & Huntsman (1938) found that the smolt run of the Apple River in 1934 showed no correlation with temperature. In a subsequent investigation of the smolt migration in the Forest Glen Brook on Cape Breton Island in 1937 and 1938, however, White (1940) found that the activity of migration tended to show a distinct positive correlation with temperature, although in both years major runs also occurred when the temperature was relatively low. In the present instance the major run which occurred as a result of the flood of 23 May took place during a period of low temperature, but comparison of the temperature and rate of catch curves suggests that during periods of comparatively constant water level there is a tendency for smolt migration to be more active during or immediately after periods of high temperature. Correlation between the rate of catch at Dalnaha and the temperature in the Sinclair Burn has been tested by means of the t test (Fisher, 1928), and it was found that $r=0\cdot27$. When the correlation between

rate of catch and temperature of 2 days previously was tested it was found that $r=0{\cdot}33$. These values of r for the number of pairs involved correspond to a probability of about 0·1. Thus it appears that there is some, but not conclusive, evidence that temperature, and particularly temperature about 2 days before, may influence the activity of smolt migration, although the greater stimulus derived from a rapid rise in water level can apparently more than offset the effect of low temperature. In the Loch Beg results the long-period fluctuations in the intensity of smolt migration are so great that they mask to a large extent the effects of daily changes in conditions and prevent a satisfactory test being made of the correlation between daily rate of catch and temperature.

In addition to its apparent influence on day-to-day fluctuations in the activity of migration, temperature may also affect the smolt migration by partly determining the time at which it occurs. It has been shown in previous papers of this series (Allen, 1940, 1941) that the time of commencement of active feeding and growth in the spring is determined by the time of the rise of temperature to 7° C. In 1938 it was found (Allen, 1941) that the temperature rose to 7° C. earlier in the Sleach Water than in the other Thurso tributaries studied, and that growth commenced correspondingly earlier. The failure of the Sleach Water stop-net to catch any smolts after 7 May indicates that the smolt migration probably occurred earlier here than in other parts of the upper Thurso system. It appears probable that the relatively early migration in this stream is associated with the earlier resumption of activity there and is therefore a consequence of the earlier rise in temperature. Thus temperature may play an important part in determining when the smolt migration takes place. It is also possible, although no data have been obtained on this point, that the temperature of the water during the period of the migration may affect the rate of smolt development, and in this way also affect the response made by the smolts to migration-producing stimuli.

(*c*) *Weather conditions.* Variations in other weather conditions have also been suggested as factors affecting the activity of smolt migration. Thus Berry (1931) found that smolts in the estuary of the River Tay in 1931 were migrating most actively in stormy weather, but the same worker (Berry, 1933) found that in 1932 the most active migration occurred in River Ness in bright weather. If weather conditions have a significant effect on the activity of migration, two observation points situated sufficiently close together to experience similar weather should show great similarities in the day-to-day fluctuations of smolt activity. The traps at Dalnaha and Loch Beg were situated only 3 km. apart in a very wide open valley, and it is very doubtful whether there were any significant differences in the weather at these two points during the period of the observations. If therefore weather played a significant part in determining the activity of migration, and consequently the rate of catch, comparison of the records of these two traps should show distinct similarities in their day-to-day fluctuations. Actually, however, comparison shows very few cases in which distinct maxima or minima in the rate of catch occur on the same day at both traps. At both traps a relatively high rate of catch was recorded on 13 May, and at both traps the catch on 18 May showed a marked fall from the preceding days, while on 10 May that at Loch Beg showed a continued fall and that at Dalnaha remained at a very low level. On the other hand, the high catches recorded at Dalnaha on 5 and 16 May correspond with relatively low catches at Loch Beg, while the increased catches at Loch Beg on 7 and 22 May correspond with greatly decreased catches at Dalnaha. Thus there does not appear to be any pronounced correspondence between the daily rates of catch at these two traps, and it appears improbable that general weather conditions played any important part in controlling the activity of migration in this river.

There is a considerable amount of evidence that a large part of the smolt migration takes place at night, and light intensity then is affected as much by the phases of the moon as by weather conditions. If, therefore, light intensity has any great effect in determining the activity of migration, the rate of catch should show more or less similar trends at all traps, and these changes should be correlated with the changes of the moon. But it has already been shown that while the activity of migration had similar trends in different parts of the river, corresponding events did not take place by any means simultaneously in all areas. Thus it is unlikely, at any rate in the present instance, that the changes of the moon had any significant effect on the activity of the smolt migration.

In Table 5 are summarized the maximum and minimum times which were recorded for smolts travelling over the various sections of the river, and the corresponding rates of movement. Mean rates of travel have not been calculated, since great variations in the rate of travel occur under different conditions, and mean values are therefore without any real significance. It is noticeable that those sections involving passage through Loch More tend to show a slower rate than the others. This may be due actually to slower travel through the still water of the loch, or perhaps also to the possibility of travel by indirect routes along the shore of the loch. The capture on 13 May on the west shore of Loch More close to the mouth of the Sleach Water of a smolt marked at Dalnaha on 27 April shows that some smolts at least do follow the indirect routes. It should be noted that all the travelling times recorded, including those shown in Table 5, exceed the actual

time by the period which elapsed between the arrival of the smolt at the second trap and its removal from it. Since the traps were usually examined daily this excess time would average approximately half a day, but it is not possible to determine its magnitude in any particular instance. Consideration of this fact shows that in some instances the maximum rates of travel may be considerably greater than those shown in Table 5. It appears, however, that 8 km. per day is probably about the maximum rate.

During the investigation a number of cases were recorded in which smolts which had been marked at one of the traps and liberated below it had found their way above the trap and were subsequently recaptured there. In most cases this occurred when a period of inactivity had elapsed between the original liberation of the fish and its recapture. Thus six smolts liberated at Dalnaha during the period 4–5 May were recaptured there during the next period of activity between 16 and 23 May; and eight smolts liberated at Loch Beg between 3 and 14 May were recaptured there during the next active period between 24 and 30 May. A few cases were, however, recorded in which smolts moved upstream during a period of active migration. Thus, two smolts marked at Dalnaha on 24 April and 12 May were recaptured there on 4 and 25 May respectively, and one smolt marked at Loch Beg on 25 May was recaptured there on 30 May. These upstream movements of smolts appear similar to those recorded by Berry (1931, 1933) and White & Huntsman (1938).

4. GROWTH

Data may be obtained from the size and appearance of the scales regarding the growth which has been made by the migrating smolts. The ages of the smolts can also be determined in this way, and Table 6 shows the numbers and percentages of smolts of different ages taken in each trap during successive periods. Since the determination of age by the examination of scales depends upon the personal judgement of the worker concerned, complete accuracy can probably not normally be attained. In the present case, while the ages of some individuals were probably incorrectly determined, it is felt that the proportions of the different age groups, as shown in Table 6, are approximately correct. It will be seen that the smolts captured had completed 1, 2 or 3 years of growth, and that those which had completed 2 years formed the great majority. As a result insufficient data are provided by the 1-year and 3-year groups to permit of accurate studies, and consequently the subsequent tables and discussion are concerned only with the smolts migrating after 2 years, although, in general, the phenomena shown by the 2-year smolts are probably also shown by the 1-year and 3-year smolts.

Table 7 shows the mean and relative deviation of the length of the smolts taken in each trap during successive 5-day periods. In each case where the data are sufficient it will be seen that the mean length shows a very gradual increase during most of the period of migration, and that at Loch Beg and Halkirk there is a sudden well-marked increase at the extreme end of the migration. This phenomenon is not shown by the Dalnaha records, but the last smolts to pass this point did so while the trap was not operating on 23 May and the following days. It is therefore not impossible that this effect occurred also at Dalnaha.

The scales of the majority of migrating smolts show at their outer edge a zone of wider circuli. This zone apparently represents the growth which has been made by the smolt in the spring before and during migration. Since, at least over short periods, the growth of the scales is proportional to the growth in length of the fish, measurement of the anterior radius of the scale both to the inner edge of this zone and to the extreme edge, enables the length of the smolt at the time of commencement of growth in the spring to be determined, and hence the amount of growth made during the spring can be calculated. Table 7 also shows the mean and relative deviation of the length of each batch of smolts at the time of commencement of growth. Since the samples taken at Dalganachan are inadequate for studies of growth, these figures have not been calculated for this trap. In all the other cases a steady reduction in the mean length at the end of the preceding winter appears to occur as the migration progresses. Consequently the increase in the actual size of the migrating smolts offers no indication of their growth. Data regarding growth can, however, be obtained from the changes

Table 5. *The maximum and minimum times taken by marked smolts to travel over the various sections of the river, and the corresponding rates of travel*

	Time (days)		Rate (km. per day)	
Section of river	Max.	Min.	Max.	Min.
Sleach Water to Loch Beg	28	4	0·6	0·09
Dalganachan to Dalnaha	17	3	2·8	0·5
Dalganachan to Loch Beg	18	2	6·2	0·7
Dalnaha to Loch Beg	27	1	4·0	0·15
Dalganachan to Halkirk	10		3·45	
Loch Beg to Halkirk	25	5	4·4	0·9

Table 6. *The number of smolts and the percentage of each age group taken in each trap in each 5-day period*

Date	Sleach Water: Total no.	Sleach Water: Percentage of age groups 1	2	3	Dalganachan: Total no.	Dalganachan: Percentage of age groups 1	2	3	Dalnaha: Total no.	Dalnaha: Percentage of age groups 1	2	3
20–24 April	.	.	.	.	1	.	100	.	38	.	95	5
25–29 April	34	12	85	3	.	.	.	.	75	.	87	13
30 April–4 May	69	9	91	.	3	.	67	33	101	3	90	7
5–9 May	2	50	50	.	1	.	100	.	61	2	90	8
10–14 May	.	.	.	.	.	.	.	.	90	2	91	7
15–19 May	.	.	.	.	1	.	100	.	83	.	99	1
20–24 May	.	.	.	.	51	4	92	4	78	4	92	4
25–29 May	.	.	.	.	.	.	.	.	.	.	.	.
30 May–3 June	.	.	.	.	.	.	.	.	.	.	.	.
4–8 June	.	.	.	.	.	.	.	.	.	.	.	.
9–13 June	.	.	.	.	.	.	.	.	.	.	.	.
Totals	105	10	89	1	57	4	91	5	526	2	92	6

Date	Loch Beg: Total no.	Loch Beg: Percentage of age groups 1	2	3	Halkirk: Total no.	Halkirk: Percentage of age groups 1	2	3	Total: Total no.	Total: Percentage of age groups 1	2	3
20–24 April	.	.	.	.	.	.	.	.	39	.	95	5
25–29 April	.	.	.	.	.	.	.	.	109	4	86	10
30 April–4 May	115	.	90	10	.	.	.	.	288	3	90	7
5–9 May	101	2	95	3	.	.	.	.	165	2	93	5
10–14 May	92	.	93	7	42	2	88	10	224	1	92	7
15–19 May	12	8	84	8	30	3	94	3	126	2	96	2
20–24 May	88	10	87	3	84	1	91	8	301	5	90	5
25–29 May	160	5	86	9	46	2	91	7	206	4	87	9
30 May–3 June	31	.	90	10	8	.	100	.	39	.	92	8
4–8 June	7	.	71	29	5	.	100	.	12	.	83	17
9–13 June	3	.	100	.	1	.	.	100	4	.	75	25
Totals	609	3	90	7	216	2	91	7	1513	3	90	7

Table 7. *The mean length in cm. at capture and at the end of the preceding winter of the 2-year smolts taken in each trap in each 5-day period. The relative deviations* (R.D.) *in the lengths are also shown*

Date	Sleach Water: No.	Mean length	R.D.	Winter length	R.D.	Dalganachan: No.	Mean length	R.D.	Dalnaha: No.	Mean length	R.D.	Winter length	R.D.
20–24 April	.	.	.	.	.	1	12·0	.	36	12·5	.	10·8	.
25–29 April	29	12·8	.	11·1	.	.	.	.	65	12·6	0·049	10·9	0·101
30 April–4 May	63	12·5	0·090	10·4	0·141	2	13·2	.	91	12·5	0·065	10·8	0·095
5–9 May	1	12·6	.	10·5	.	1	12·3	.	55	12·5	0·061	10·5	0·118
10–14 May	.	.	.	.	.	.	.	.	82	12·7	0·066	10·7	0·141
15–19 May	.	.	.	.	.	1	13·4	.	82	13·0	0·065	10·4	0·135
20–24 May	.	.	.	.	.	47	13·0	.	72	12·9	0·067	10·2	0·139
25–29 May	.	.	.	.	.	.	.	.	.	.	.	.	.
30 May–3 June	.	.	.	.	.	.	.	.	.	.	.	.	.
4–8 June	.	.	.	.	.	.	.	.	.	.	.	.	.
9–13 June	.	.	.	.	.	.	.	.	.	.	.	.	.

Date	Loch Beg: No.	Mean length	R.D.	Winter length	R.D.	Halkirk: No.	Mean length	R.D.	Winter length	R.D.
20–24 April	.	.	.	.	.	.	.	.	.	.
25–29 April	.	.	.	.	.	.	.	.	.	.
30 April–4 May	104	12·9	0·066	11·5	0·121	.	.	.	.	.
5–9 May	96	12·9	0·071	11·4	0·132	.	.	.	.	.
10–14 May	86	13·0	0·065	11·1	0·138	37	13·2	.	10·5	.
15–19 May	10	13·3	.	11·6	.	28	13·2	.	10·0	.
20–24 May	76	13·1	0·072	10·0	0·177	76	13·3	0·056	10·0	0·158
25–29 May	137	13·1	0·086	10·0	0·156	42	13·3	0·058	9·5	0·135
30 May–3 June	28	14·1	.	10·6	.	8	13·3	.	9·8	.
4–8 June	5	14·2	.	10·6	.	5	14·3	.	11·0	.
9–13 June	3	14·8	.	10·1	.	.	.	.	.	.

in the average increment in growth which has been made during the spring. These increments are shown in Table 8. It will be seen that in all cases the increment increases steadily during the period of observations. If all smolts were growing at the same rate, or had commenced growth at the same time, the rate of increase of the increment would equal the rate of growth of the smolts. The apparent average growth rate obtained in this way has been determined for each trap by dividing the period of the observations into two, and determining the mean spring increment of growth for each of these periods, and dividing the difference between these by the interval between the mean dates. In doing this all samples of fewer than 25 smolts in any 5-day period have been ignored. The results obtained at the different traps show considerable variations, but the average value is similar to but rather higher than the growth rate found for salmon parr in the Thurso system during their second year (Allen, 1941).

Owing to the two possible sources of error referred to above, the apparent rates of growth obtained in this way, and shown in Table 8, probably do not represent exactly the true rate of growth. The fact that the average smolts passing the traps early and late in the run had made different amounts of growth in their preceding years suggests that they might continue to show some differences in their growth which would prevent their increments being truly comparable. All the traps, but particularly those at Loch Beg and Halkirk, were receiving smolts which had originated in various parts of the river system, and it is probable that, at least in some cases, the time of commencement of growth differed in different areas. It has already been shown (Allen, 1941) that as a result of the earlier rise in temperature growth commenced in the Sleach Water in 1938 earlier than in some other parts of the upper Thurso system. If the proportions in which smolts from different areas were arriving at a trap varied during the run, any local differences in the time of commencement of growth would tend to prevent the growth increments being truly comparable.

Table 8. *The mean increment of growth made in the spring of migration by the 2-year smolts taken in each trap in each 5-day period: also the average rate of increase of increment in each trap*

	Sleach Water				Dalnaha			
Date	Incr.	Mean incr.	Mean date	Rate cm./day	Incr.	Mean incr.	Mean date	Rate cm./day
20–24 April	.	.	.	.	1·6			
25–29 April	1·7	.	28·9 April	0·21	1·6	1·66	28·9 April	
30 April–4 May	2·1	.	30·8 April		1·7			
5–9 May	2·1*	.	.	.	1·9			0·040
10–14 May	.	.	.	.	2·0	2·28	14·5 May	
15–19 May	.	.	.	.	2·6			
20–24 May	.	.	.	.	2·6			
25–29 May	.	.	.	.	.	.	.	.
30 May–3 June	.	.	.	.	.	.	.	.
4–8 June	.	.	.	.	.	.	.	.
9–13 June	.	.	.	.	.	.	.	.

	Loch Beg				Halkirk			
Date	Incr.	Mean incr.	Mean date	Rate cm./day	Incr.	Mean incr.	Mean date	Rate cm./day
20–24 April	.	.	.	.	.	.	.	.
25–29 April	.	.	.	.	.	.	.	.
30 April–4 May	1·5	.		.	.	.	.	.
5–9 May	1·5	1·61	7·0 May	.	.	.	.	.
10–14 May	1·9				2·7			
15–19 May	1·7*			0·082	3·2	2·93	14·4 May	
20–24 May	3·1				3·3			0·059
25–29 May	3·1	3·15	25·7 May		3·8	3·48	23·7 May	
30 May–3 June	3·5	.	.	.	3·5*	.	.	
4–8 June	3·8*	.	.	.	3·3*	.	.	.
9–13 June	4·7*	.	.	.	.	.	.	.

* Denotes samples of less than 25 fish.

The most accurate data regarding the rate of growth of migrating smolts are obtained from those which were marked and recaptured. Most of the smolts marked in this investigation could only be identified as members of a batch and not as individuals, and therefore do not provide satisfactory data regarding growth. A number of smolts were, however, marked either with tags or with unique combinations of fin clippings, and could be identified

as individuals. Table 9 summarizes the data obtained from such of these as were recaptured more that 5 days after being originally marked. The majority of these smolts were recaptured at Loch Beg, and it will be seen that their rate of growth was only about one-third of the rate of increase in increment at this station as shown in Table 8. It is therefore possible that the rate of increase in increment may generally be in excess of the actual rate of growth, and this would be the consequence of a tendency for the smolts passing any point to have commenced their growth progressively earlier as the migration proceeds.

Table 7 shows that there is a tendency for those smolts which were largest at the end of their second winter to migrate first, and for the average size at the end of the second winter to decrease steadily as the run continues. On the other hand, the size of the smolts actually migrating tends to increase slightly, although, apart from the sharp increase at the extreme end of the run, the change in size of migrating smolts is small compared with the changes in the size at the end of the second winter. Thus

Table 9. *The average growth of smolts individually marked and subsequently recaptured*

No. of smolts	Mean increment in length cm.	Mean period days	Mean rate of growth cm./day
12	0·35	13·0	0·027

growth made in the spring tends to make the size of the smolts more uniform at migration. That this effect applies also within batches of smolts migrating at the same time is shown by comparison of the relative deviations of the actual lengths and of the winter lengths. In most cases (Table 7) the relative deviation in length at migration is approximately half the relative deviation in winter length.

This tendency for growth made in the spring to make the size at migration more uniform has been recorded for the salmon on several other rivers. Pentelow, Southgate & Bassindale (1933) found that in the smolt migration in the River Tees in 1930 and 1931 those smolts which had made no growth in the spring were of the same average size at migration as those which had made growth, although the latter had averaged about 0·75 cm. less in length at the end of the preceding winter. They concluded 'in general it is necessary for smolts to attain a physiological condition which is connected with a certain size before they migrate'.

Went (1938, 1940, 1941) and Frost & Went (1940) found similar phenomena in the salmon of the Rivers Shannon, Liffey and Ballisodare, and reached the conclusion that 'the parr must attain some physiological condition associated, at least as an index, with a minimum size before the smolt migration takes place'. Nall (1938) found the same phenomenon in the migrating smolts of the River Avon, but points out that it is only the mean sizes at migration of the two groups which correspond, and that actually many fish which were well above this size at the end of the preceding winter continue to grow while in fresh water, and that many fish which were below this size at the end of the preceding winter migrate without further growth. It thus does not appear that size is in itself the factor which determines when smolts migrate. He suggests that it is the 'vigorousness' of the individual salmon which determines their time of migration. The more vigorous individuals grow better in their early years and also 'tend to make a more immediate response to the migratory impulse, to descend earlier in the season, and to push on to salt water without lingering on the way to feed (and make extra growth), whereas the less vigorous individuals tend to delay their descent and to feed (and grow) on their downward journey'.

The investigations referred to above have been based on the examination of the scales, either of migrating smolts or of adult salmon, and in each case the smolts have been divided into only two categories according to whether or not they show on their scales any spring growth. Table 10 shows for the four largest samples the number of smolts in each 5-day period which had at the edge of their scales various numbers of wide circuli. The data suggest that a genuine distinction may be drawn between smolts which make spring growth and those which do not. In both the Loch Beg and Dalnaha records there appears, even during the later part of the run, to be a small number of smolts showing no growth at the edge of their scales, as distinct from the majority having two to eight wide circuli. During the early part of the run it is not, however, possible to distinguish these two categories, since the normal distribution of those ultimately showing growth will then include some which have not yet made any growth. In this case also (as was found by Pentelow and Nall) the proportion of smolts showing no growth at the edge of their scales tends to decrease as the run progresses, and during the later part of the run almost all the smolts have made some growth. The reduction which occurs between the end of the second winter and the time of migration in the relative deviation in length shows that among the smolts which make spring growth the effect of this growth is to tend to make the size at migration more uniform.

It is clear that there is a general tendency for the more rapidly growing smolts to migrate earlier. This has long been known to apply between smolts migrating at different ages, and the data referred to above show that it applies also within single age groups. These effects indicate clearly that there is a close relationship between size and time of migra-

tion, but it is evident that there is no critical size at which all smolts migrate. Although in general the most rapidly growing smolts in any river migrate after 1 year, and more slowly growing ones after 2 or more years, the actual size at migration is usually considerably less for the 1-year smolts than for the older smolts. Further, in many instances, a large proportion of the smolts which migrate when 2 years old make further growth in the spring of their migration, although at the end of the preceding winter they were already larger than those which migrated when 1 year old. This has been clearly shown by Nall (1938). There also appear to be considerable differences in the size at which smolts of the same age migrate from different rivers. These facts suggest that the relation between size and time of migration is by no means direct, and that there is no critical length at which migration takes place.

The factors which determine when a young salmon migrates to sea as a smolt are obviously of great complexity. The results described in the earlier part of this paper show that active migration only occurs when a suitable stimulus is provided by the environment, but they also show that the extent of the reaction to the stimulus depends on the degree of 'smolt development' of the salmon, that is, the degree to which it has become susceptible to such stimuli. The data indicate that there is some relation between 'smolt development' and the size of the salmon, but since, in most cases, the smolt migration only takes place at one season of the year—the spring—it is evident that some seasonal factor, probably climatic, must provide the necessary stimulus to 'smolt development', but that it can only initiate development in salmon which are otherwise in the correct physiological condition. It is this physiological condition which is apparently related to the size of the salmon, although the relation is evidently not direct. If this relation were direct, not only would entire size groups of smolts migrate completely together, showing no overlap with the size range of smolts migrating at other times, but also, in most rivers, the very great majority of smolts would migrate at the beginning of their second spring without making further growth, since they are already considerably larger than those which migrated in their first spring. The evidence shows clearly that neither of these phenomena normally occur, and therefore the relation between size and the physiological condition necessary for smolt development is not direct.

Nall (1938) has suggested that the vigorousness of the salmon determines when smolt development occurs. But this hypothesis would only explain the phenomenon if vigorousness increased with size, since if it remains constant those smolts which were

Table 10. *The distribution of wide circuli at the edge of the scales of 2-year smolts caught in each 5-day period: also the percentage in each sample having no wide circuli at the edge of the scale*

Station and date	No. of circuli 0	1	2	3	4	5	6	7	8	9	10	11	12	Mean no.	Percentage with 0
Sleach Water															
25–29 April	4	3	4	11	4	3	.	.	.	.	.	.	.	2·6	14
30 April–4 May	2	3	11	17	16	10	2	.	.	.	.	.	.	3·3	3
5–9 May	.	.	.	1	.	.	.	.	.	.	.	.	.	3·0	0
Dalnaha															
20–24 April	2	3	15	9	4	1	.	.	.	.	.	.	.	2·5	6
25–29 April	8	4	26	17	6	2	1	.	1	.	.	.	.	2·4	12
30 April–4 May	4	10	27	29	13	5	2	.	.	.	.	.	.	2·7	4
5–9 May	3	4	9	19	13	6	.	.	.	.	.	.	.	3·0	6
10–14 May	4	1	21	26	16	9	2	2	.	.	.	.	.	3·2	5
15–19 May	2	.	9	21	26	18	6	1	1	.	.	.	.	3·9	2
20–24 May	1	2	6	15	21	20	4	2	.	1	.	.	.	4·0	1
Loch Beg															
30 April–4 May	16	10	27	29	12	8	1	.	.	.	.	.	.	2·4	16
5–9 May	15	5	26	35	14	3	.	.	.	.	.	.	.	2·4	15
10–14 May	10	4	19	26	21	5	.	3	.	.	.	.	.	2·8	11
15–19 May	2	.	.	7	1	1	.	.	.	.	.	.	.	2·7	18
20–24 May	1	.	3	13	24	16	13	7	8	.	.	1	.	4·7	1
25–29 May	3	2	3	13	27	50	29	10	1	1	.	.	.	4·8	2
30 May–3 June	.	.	2	2	6	8	3	2	1	1	.	.	1	5·2	0
4–8 June	.	.	.	.	1	2	2	.	.	.	.	.	.	5·2	0
9–13 June	.	.	.	.	.	.	1	1	.	1	.	.	.	7·3	0
Halkirk															
10–14 May	1	.	4	8	13	3	7	.	.	.	.	.	.	3·9	3
15–19 May	.	.	.	3	10	7	7	2	.	.	.	.	.	4·8	0
20–24 May	.	1	5	9	19	16	19	5	1	1	.	.	.	4·7	0
25–29 May	.	.	.	2	4	14	12	7	2	1	.	.	.	5·7	0
30 May–3 June	.	.	.	.	1	4	2	1	.	.	.	.	.	5·4	0
4–8 June	.	.	.	.	.	3	1	.	1	.	.	.	.	5·8	0

not sufficiently vigorous to be stimulated to smolt development in their first spring would not be so in their subsequent springs. Further, in order to explain the phenomenon, vigorousness must vary not only with innate differences in growth rate which cause the differences in size of fish of the same age living in the same environment, but also with differences in growth rate imposed by environmental conditions. This latter condition is necessary, since comparison of the salmon stocks of different rivers shows that in general the average age at migration shows a strong negative correlation with the rate of growth. Thus the hypothetical quality of 'vigorousness' is so closely related to the size of the smolts that it does not appear that the explanation simplifies the problem of the relation between size and smolt development.

Thus a complex chain of causes appears to determine when and with what velocity an individual salmon carries out its smolt migration; and there are two factors in this chain about which no satisfactory data exist. These are, first, the cause of the physiological condition necessary for smolt development, and its relation to size, and secondly, the nature of the environmental stimuli producing smolt development in salmon in suitable condition.

5. SMOLT DEVELOPMENT

While no precise measurement is possible of the development of the susceptibility to migration-producing stimuli, the change in behaviour is accompanied by well-marked changes in appearance, which are capable of more or less exact measurement. The principal changes in appearance are the development of a silvery coating over the whole body and changes in colour of some of the fins. The development of the silvery coat is not easily divided into stages, and is therefore not suitable for study, but the change in colour of the pectoral fins from yellow to black is very distinct, and is easily divided into four stages. This change was therefore used as a measure of the degree of smolt development. It cannot be assumed that the changes in appearance always bear the same relation to the changes in behaviour, and it is probable that individual fish may differ in this respect. Study of the changes in appearance does, however, provide an indication as to the general trends of the smolt development.

The four stages distinguished in the change of fin colour were: (1) entirely yellow; (2) yellow shaded with black; (3) black with a yellow tinge; (4) entirely black. These stages were given corresponding numerical values. In nearly all cases the smolts caught in the traps showed at least a trace of silvering of the scales, but a few smolts were captured in which this silvering had not commenced; these always had yellow pectoral fins, and this degree of smolt development was given the value of 0. Table 11 shows for each 5-day period the average weight, condition factor and degree of smolt development of the smolts taken in each trap. The condition factor has been calculated by means of the formula $(W \times 10^4)/L^3$, where W is the weight in grams and L the length in centimetres. The condition factors of individual fish were only determined to the nearest 5 units, since any greater degree of accuracy did not appear to be justified in view of the probable errors involved in measuring the weights and lengths of the fish.

The table shows that during the progress of the run there was at all traps a gradual increase in the degree of development reached by the smolts. This result is in agreement with the observations of Berry (1931) and White & Huntsman (1938). The table also shows that there are striking differences in the degree of development reached at the same time by migrating smolts in different parts of the river. It is also apparent that active migration commences before the smolts have fully developed their smolt livery. It appears probable that susceptibility to migration-producing stimuli and the smolt livery commence to develop together.

Information regarding the rate at which individual smolts develop their livery can be obtained from the records of marked fish. Table 12 shows for each 5-day period the average degree of development of smolts arriving at Loch Beg after having been marked at Dalnaha, compared with the development of the smolts passing Dalnaha in the period of their departure. It is clear that during any arrival period there is a tendency for those smolts which have been longest on the way to be most highly developed. This is particularly well shown by the smolts which arrived between 20 and 29 May. Similarly, among the smolts leaving Dalnaha during any period the degree of development reached on arrival shows a progressive increase with the time taken on the journey. This is clearly illustrated by the smolts leaving Dalnaha during the period 25 April–4 May.

From these facts it is evident that development of the smolt livery continues during the actual migration. If it is assumed that the average degree of development reached at Dalnaha was the same for all smolts, regardless of the time taken to travel to Loch Beg, then the rate of development can be calculated for smolts travelling between these two stations. Table 13 shows the apparent rate of development obtained in this way for smolts arriving at Loch Beg during the period 20–29 May. The very constant results obtained suggest strongly that the basic assumption is correct, and that these figures do indicate the actual rate at which smolt development was proceeding, and that the average rate did not change during the period of these observations. Therefore the gradual increase in the degree of

Table 11. *The mean weight in grams, mean condition factor (K), and mean degree of smolt development (S), of the 2-year smolts taken in each trap in each 5-day period*

	Sleach Water			Dalganachan			Dalnaha			Loch Beg			Halkirk		
Date	Mean wt.	*K*	*S*	Mean wt.	*K*	*S*	Mean wt.	*K*	*S*	Mean wt.	*K*	*S*	Mean wt.	*K*	*S*
20–24 April	.	.	.	.	.	.	18·2	92	.	.	.	.	.	.	.
25–29 April	19·6	92	.	.	.	.	18·5	93	.	.	.	.	.	.	.
30 April–4 May	18·3	90	2·2	21·0	90	1·0	18·6	94	1·4	19·8	91	2·1	.	.	.
5–9 May	18·5	90	2·0	16·0	90	1·0	18·3	94	1·5	19·9	91	2·2	.	.	.
10–14 May	.	.	.	.	.	.	18·9	92	1·7	19·7	89	2·6	21·4	92	2·0
15–19 May	.	.	.	26·5	110	1·0	19·8	89	1·6	21·4	90	2·5	22·0	95	1·6
20–24 May	.	.	.	20·3	92	1·9	19·4	90	1·9	20·4	91	2·6	22·5	95	2·2
25–29 May	.	.	.	.	.	.	.	.	.	21·1	92	2·5	22·1	94	2·3
30 May–3 June	.	.	.	.	.	.	.	.	.	27·1	93	2·8	22·5	93	2·7
4–8 June	.	.	.	.	.	.	.	.	.	27·3	92	2·8	26·8	93	2·8
9–13 June	.	.	.	.	.	.	.	.	.	30·0	90	3·0	.	.	.

Table 12. *The degree of development (S) of 2-year smolts, marked at Dalnaha, on arrival at Loch Beg, compared with their degree of development at departure*

		Date of arrival																	
		30 April–4 May		5–9 May		10–14 May		15–19 May		20–24 May		25–29 May		30 May–3 June		4–8 June		9–13 June	
Date of departure	*S* at departure	No.	*S*	No.	*S*	No.	*S*	No.	*S*	No.	*S*	No.	*S*	No.	*S*	No.	*S*	No.	*S*
20–24 April	.	2	1·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25–29 April	.	9	1·7	7	2·3	1	2·0	1	2·0	2	2·5	.	.	.	.	.	.	.	.
30 April–4 May	1·4	3	1·0	7	1·7	4	2·7	.	.	1	3·0	1	3·0	.	.	.	.	.	.
5–9 May	1·5	.	.	.	.	3	2·0	.	.	3	3·0	3	3·0	.	.	.	.	.	.
10–14 May	1·7	.	.	.	.	.	.	.	.	4	2·7	5	2·6	.	.	.	.	.	.
15–19 May	1·6	.	.	.	.	.	.	.	.	4	2·2	4	2·2	1	3·0	.	.	.	.
20–24 May	1·9	.	.	.	.	.	.	.	.	1	2·0	18	2·2	2	2·5	.	.	1	2·0

Table 14. *The number and condition factor (K) of 2-year smolts of each degree of development taken in the three principal traps in each 5-day period*

		Date of capture																		
		30 April–4 May		5–9 May		10–14 May		15–19 May		20–24 May		25–29 May		30 May–3 June		4–8 June		9–13 June		
Station	Degree of develop-ment	No.	*K*	No.	*K*	No.	*K*	No.	*K*	No.	*K*	No.	*K*	No.	*K*	No.	*K*	No.	*K*	Mean
Dalnaha	1	50	95	29	94	35	92	40	90	18	92	.	.	.	.	.	.	.	.	92·8
	2	34	94	23	94	36	90	33	88	44	89	.	.	.	.	.	.	.	.	90·9
	3	1	85	3	90	10	94	8	87	10	87	.	.	.	.	.	.	.	.	89·5
Loch Beg	1	20	91	16	95	6	91	3	97	2	97	3	103	.	.	.	.	.	.	93·4
	2	51	92	43	91	33	90	2	87	25	90	67	92	5	96	1	90	1	90	91·1
	3	30	89	31	89	37	88	2	87	47	90	65	92	18	92	4	92	1	90	90·0
	4	1	85	4	88	8	87	3	88	3	92	2	92	3	90	.	.	1	90	89·8
Halkirk	1	.	.	.	.	5	94	13	97	1	100	1	100	.	.	.	.	.	.	96·2
	2	.	.	.	.	26	92	13	95	59	94	28	95	2	90	1	85	.	.	93·9
	3	.	.	.	.	6	90	1	85	15	94	13	90	6	94	4	95	.	.	92·4
	4	.	.	.	.	1	85	1	100	.	.	.	.	.	.	.	.	.	.	92·5

development shown in Table 11 is probably due to the smolts having been developing for progressively longer periods as the run continues. Since the rate of development is shown in Table 13 to be the same for smolts that have taken very different times over the journey between Dalnaha and Loch Beg, it does not appear that there is any correlation between the rate at which smolts develop and the rate at which they travel. The average rate of increase in degree of development at any trap during the run, about 0·02 per day, is only about a quarter of the rate of development of individual smolts as shown in Table 13, and therefore the migrating smolts must have commenced their development progressively later as the run proceeds.

Since the average rate of development remains constant, the increase with time in the degree of development at any point on the river must be due to an increase in the average time for which the smolts have been developing. It is therefore probable that on the average the smolts passing any

Table 13. *The mean rate of development of 2-year smolts, marked at Dalnaha, arriving at Loch Beg between 20 and 29 May*

Date of departure	Increase in development	Mean interval days	Mean rate of development
30 April–4 May	1·60	21·5	0·074
5– 9 May	1·48	18·5	0·080
10–14 May	1·00	12·8	0·078
15–19 May	0·67	6·5	0·103
20–24 May	0·30	4·9	0·061

point have come from progressively farther up the river as the run proceeds. Since, however, it appears that the late arrivals have been developing for a shorter period, it is probable that the factor which causes the smolts to commence their metamorphosis and migration, whatever it may be, operates progressively farther up the river, and that the average smolt begins these processes progressively later upstream. As has been shown earlier, the actual migratory movements depend upon various environmental factors and may occur differently in different sections of the river, but the average commencement of susceptibility to these factors conforms to the principle outlined above. It is evident from the great variations in the degree of development shown by individual smolts at the same time and place that there are large individual variations in the time of commencement of development.

The consistent differences in the degree of development of the smolts at different traps are the result of differences in the origin and environment of the smolts concerned. But it is probable that the degree of development of the smolts passing through any trap provides, when averaged over the whole run, an index of the average distance which those smolts have travelled. The smolts caught in the Sleach Water show a much higher degree of development than those caught at Dalnaha at the same time, but it is very doubtful whether these results can properly be compared. It has already been shown that the complete spring complex of events took place much earlier in the Sleach Water than in other parts of the upper Thurso system, and it seems that during the period under consideration the last of the smolts were passing out of the Sleach Water while at Dalnaha the run was only partially developed. If the last smolts caught at Dalnaha are compared with the last significant catches in the Sleach Water, it will be seen that the difference in the degree of development is comparatively slight. It is probable that comparison of corresponding sections of the river in this way provides a fairly satisfactory substitute for a comparison of whole runs, and that therefore the average degree of development was similar in the Sleach Water and at Dalnaha. On the other hand, the smolts caught at Loch Beg show, when averaged over the whole run, a much higher degree of development than those caught at Dalnaha. This probably arises from the greater distance, and hence time, which the majority of smolts had travelled to reach the former trap. It is probable that very few of the smolts originated in Loch More and the portion of the river immediately below it, and hence most of the smolts passing this trap originated either above Dalnaha or at an equivalent distance up one of the other tributaries of the loch. In addition, at least the early part of the run past Loch Beg contained a certain proportion of smolts which originated in the Sleach Water, and which were more highly developed than those from the upper part of the Thurso River.

The few smolts taken at Dalganachan prior to 20 May were consistently less developed than those taken at Dalnaha at the same time. The larger samples taken between 20 and 24 May show, however, the same degree of development as those at Dalnaha. It has been shown that this trap probably obstructed the migration, and it is therefore probable that these smolts would normally have passed this point earlier and at a lower degree of development. Thus, the results obtained at the four highest observation points tend to show that at corresponding periods in the run the degree of development shown by the smolts increases in a downstream direction, and this result is in accordance with the hypothesis outlined earlier.

On the other hand, the degree of development of smolts passing Halkirk is consistently lower than that of those passing Loch Beg. This may, however, arise from the large proportion of the Halkirk smolts which originated in the main river between the two traps. Among 229 smolts taken at Halkirk only 14, or 6·1 %, had been marked at Loch Beg, and therefore, since about 18 % of the smolts passing

Loch Beg were caught and marked, only about one-third of the smolts passing Halkirk had originated above Loch Beg. It is possible that these smolts originating between the two traps and having therefore moved a comparatively short distance are responsible for the relatively low degree of development shown at Halkirk. It seems therefore that the following conclusion can be drawn from the study of the development of the smolt livery. Development of the livery proceeds in association with development of the susceptibility to migration-producing stimuli. Migration may take place under suitable conditions as soon as development has commenced, and development continues while the smolt migrates. The average rate of development appears to remain more or less constant during the progress of the run, but it is probable that development commences progressively later farther upstream.

The colour changes which have been discussed above are the most obvious features of the physical changes which occur in association with the migration of the young salmon to the sea. It appears to be generally believed that in addition a reduction in condition takes place during the process. This belief can be tested by the data from the present investigation. Table 11 shows the average condition factor of the smolts taken in each trap during each 5-day period. Comparison of these results with the condition factors found for young salmon of the Thurso system in all stages before migration (Allen, 1941) shows that the condition of the migrating smolt is consistently lower than at any previous stage after the emergence of the fry. This result is similar to that obtained by Hoar (1940) in regard to the salmon of the Mangaree River.

Since only slight changes in the degree of smolt development occur at any trap during the run, the absence of well-marked changes in condition does not prove that the development of the smolt livery is not accompanied by changes in condition. Direct comparisons have therefore been made between the condition factor and the degree of smolt development, and the results for the three observation points are shown in Table 14, which shows that, particularly when the smaller samples are neglected, there is a clear-cut tendency for the more developed smolts in all traps and at all times to have a lower condition factor, and hence it is probable that the development of the smolt livery is actually accompanied by a decrease in the condition factor. Although the decrease in the condition factor is not very great, the contrast between the condition of the smolts and that of the non-migrating salmon is increased by the fact that the smolts are metamorphosing and losing condition, while at the same time the non-migrating fish that are not metamorphosing are increasing in condition.

Table 14 indicates also that certain changes in condition occur which are unrelated to the development of the smolt livery. These changes were masked when the smolts were considered as a whole. During the early part of the run there is a steady decrease in condition in all parts of the river, and this is succeeded by a period of increasing condition. There appears to be a tendency for the increase in condition to commence progressively farther up the river. This reversal in the change in condition factor is similar to that observed by Hoar, who, however, ascribed the early decrease to the effect of the development of the smolt livery. The data given in Table 14 show that this is not the case, and other factors therefore have to be found to account for these changes. The table also shows that the average condition of the smolts is similar at Dalnaha and Loch Beg, but that those passing Halkirk have a considerably higher average condition factor. This is probably another result of the fact that the smolts passing Loch Beg and Dalnaha were largely drawn from the same population, while a large proportion of those caught at Halkirk originated below Loch Beg and had therefore been living under somewhat different conditions.

6. SUMMARY

1. A study of the migration of the smolts in the Thurso River system in 1938 was made by observing the number, size and development of the smolts passing through four traps situated at different points of the system.

2. Throughout the river the activity of migration declined for a time after the commencement of observations, and then after a period of almost no activity increased again to a maximum, during which practically all the smolts left the upper part of the river.

3. Corresponding events usually occurred about 8 days earlier above Loch More than below it.

4. The smolts did not appear to travel in permanent shoals. Individuals liberated at any trap on the same day arrived at the next trap over a considerable period.

5. Waves of active migration due probably to moving stimuli appear to travel slowly down the river.

6. In addition to the associated changes in appearance, smolt development consists of the development of susceptibility to migration-producing stimuli. The difference in the degree of development of different individuals will affect the extent to which they respond to stimuli, and probably accounts for the wide divergence observed in the rate of travel of individual smolts. Observed rates of travel ranged from 0·1 to 6 km. per day.

7. The nature of the factors stimulating migration is considered. Rises in water level appear definitely to act as stimuli, and it is probable that

temperature also has an effect on the activity of migration. The passing of other actively migrating smolts also seems to act as a stimulus.

8. Scale examination showed that the great majority of smolts migrated after 2 years, and only a very small proportion after 1 and 3 years.

9. The spring increment of growth, as shown on the scales, increased rather more rapidly than the average growth rate of individually marked smolts, suggesting that the late migrants may have commenced their growth earlier.

10. The effect of spring growth is to make the actual size at migration more uniform than it was at the end of the preceding winter.

11. The relation between size and migration is considered and shown to be extremely complex. There is, however, an apparent relation between size and the onset of smolt development which causes a salmon to migrate in response to suitable external stimuli.

12. The degree of smolt development was determined from the colour of the pectoral fins; the average rate of development was found to be about 0·08 per day, on a colour scale where 4·0 represents full development.

13. The degree of development of the smolts passing any one point increased, although more slowly than the average individual rate. This suggests that time for which the smolts passing any point had been developing increased as the run proceeded, probably due to the smolts having come from farther up the river.

14. Direct comparison shows that smolt development is associated with a slight decrease in the condition factor. There are also fluctuations in condition during the run which are not associated with smolt development.

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REFERENCES

Allen, K. R. (**1940**). 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 1. Growth in the river Eden.' J. Anim. Ecol. 9: 1–23.

Allen, K. R. (**1941**). 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 3. Growth in the Thurso system, Caithness.' J. Anim. Ecol. 10: 273–95.

Berry, J. (**1931**). 'Report of an investigation of the migration of smolts in the river Tay during spring 1931.' Fisheries, Scotland, Salmon Fish. No. 6, 1–21.

Berry, J. (**1933**). 'Notes on the migration of salmon smolts from Loch Ness; summer 1932.' Fisheries, Scotland, Salmon Fish. No. 1: 1–12.

Bull, H. O. (**1930**). 'The smolt descent on the river Tyne.' Ann. Rep. Dove Marine Lab. 19: 37–66.

Bull, H. O. (**1931**). 'The smolt descent on the river Tyne, 1931.' Ann. Rep. Dove Marine Lab. 20: 32–42.

Fisher, R. A. (**1928**). 'Statistical methods for research workers.' 2nd ed., London.

Frost, W. E. & Went, A. E. J. (**1940**). 'River Liffey survey III. The growth and food of young salmon.' Proc. Roy. Irish Acad. 46B: 53–80.

Hoar, W. S. (**1940**). 'The weight-length relationship of the Atlantic salmon.' J. Fish. Res. Bd. Can. 4: 441–60.

Nall, G. H. (**1938**). 'Notes on scales from Avon salmon smolts in 1938.' Rep. Avon Biol. Res. 6: 16–26.

Pentelow, F. T. K., Southgate, B. A. & Bassingdale, R. (**1933**). 'The relation between the size, age and time of migration of salmon and sea trout smolts in the river Tees.' Min. Agric. Fish., Fish. Invest. Ser. 1, Vol. 3, No. 4, 3–10.

Went, A. E. J. (**1938**). 'Salmon of the river Shannon.' Proc. Roy. Irish Acad. 44B: 261–322.

Went, A. E. J. (**1940**). 'Salmon of the river Shannon.' J. Dep. Agric. Eire, 37: 254–310.

Went, A. E. J. (**1941**).. 'Salmon of the Ballisodare river. II. Age and growth.' Sci. Proc. Roy. Dublin Soc. 22: 327–44.

White, H. C. (**1940**). 'Factors influencing descent of Atlantic salmon smolts.' J. Fish. Res. Bd. Can. 4: 323–6.

White, H. C. & Huntsman, A. G. (**1938**). 'Is local behaviour in salmon heritable?' J. Fish. Res. Bd. Can. 4: 1–18.

REVIEWS

THE POPULATION DYNAMICS OF A BIRD

David Lack (1943). *The life of the robin.* 200 pp., 10 half-tone plates, 2 text-figures. H. F. and G. Witherby Ltd., 326 High Holborn, London. Price 7*s.* 6*d.*

Recently the term 'popular bird book' has become almost a stigma in the eyes of professional and the best of amateur zoologists. The demand by the public for readable books on popular natural history is immense, and so a considerable output of books of this type is maintained by the publishers. The results have fallen mainly into two categories: books which 'write-up' (or rather 'write-down') the results of scientific work, and books which weave a narrative around a collection of animal photographs. The latter often have the virtue of first-hand observation to recommend them. On the whole, however, these categories are ephemeral or redundant or both.

Such a criticism might well have been milder, if the reviewer had not read this book. As a popular book (but written by a professional zoologist) it is so far ahead of the usual run that it naturally reflects discredit on them. The outstanding merits of this book are these: it has some fundamental and original research to communicate; its data are drawn from intensive field observation supplemented by critical experimenting; the interpretation of the results is based on an adequate knowledge of reproductive physiology and the wider problems of behaviour; finally, the style of writing is straightforward and readily understandable to non-scientific readers without being reduced to baldness. Diversification by old and apt citations is judiciously indulged in, where even a slight over-indulgence would have been fatal.

The book shares with the early works of Eliot Howard the distinction of showing how little is yet known about the commonest of British birds. The life history of the robin, patiently worked out by colour ringing, which made it possible to identify individuals, is of great interest to the ecologist. To many aspects of his subject, such as vital statistics generally and the composition of populations, the limitation of densities and the relationships between inter- and intraspecific competition, this technique is the only one applicable, and, though laborious, has an almost untouched fund of facts to elicit.

To take an example from a small part only of this book: the discussion of the average expectation of life and of age composition in robin populations at different times reveals the very rapid turn-over in individuals. It is calculated that each pair of robins must produce a mean number of six fledglings each year to make good the high rate of mortality. Of one hundred fledglings an average of seventy-seven is expected to die in their first year of life. For adults the yearly figure is lower because of their greater experience, but even so sixty-two out of every hundred die in each year. Thus the average expectation of life for a robin is slightly less than a year in youth and slightly more in maturity. Hardly any individual can reach the end of its reproductive life before it dies, which is in striking contrast to human beings and to laboratory animals. These figures emphasize well the dynamic nature of population equilibria, which the ecologist studies. There are important implications also for those who study the genetics of wild populations and the role of selection pressure in guiding evolutionary progress.

However, this part of the book is not only a small one; it is not even based upon the main body of the research work. The greater part is devoted to elucidating the different phases of territorial and breeding behaviour of the robin. Here there is much that is new knowledge, much that was only vaguely outlined by previous students, and it is impossible for a reviewer to do more than draw attention to some of the points which seem to him outstanding.

The careful working out of the principles of recognition between the sexes and the relation of this to physiological condition is most interesting, especially the part which deals with the recrudescence of sexual behaviour in the late summer and autumn. It seems remarkable enough that the swing-over from late autumn behaviour, in which the male reacts aggressively to all trespassers, to winter pairing behaviour, in which each male learns to tolerate another bird in his territory, can be effected with precision: it is even more interesting to find that this is done by a process almost of trial and error, in which the male's aggressiveness is toned down as far as one bird is concerned and he learns to recognize his mate by her behaviour. At the same time the hen must learn the boundaries of her new territory and become aggressive in its defence. All these adjustments must take place some months before any signs of breeding behaviour appear.

The fact, foreshadowed by Burkitt and amply confirmed by these results, that nearly all male robins are non-migratory, while between two-thirds and three-quarters of the females migrate, shows a half-way stage in the development of resident habits in a species, which was probably entirely migratory at one time. This condition will no doubt be established for other British species when sufficient data have been collected.

Finally, lest the reader should feel that the book is almost entirely concerned with the elucidation of facts, he finds something considerable to chew upon in the last chapter on instinct, which shows the general thoughts running through the author's mind while the work was in progress, and gives it a purposive and integrative stamp so rarely found in popular books.

The method of giving references by pages at the end of the book and so doing away with the disruptive effect of many citations in the text might well be adopted more widely in this kind of publication. The photographs illustrate the text well and have all been reproduced satisfactorily, except the frontispiece.

Ecologists will wish this book to be successful, and will hope that it will explain to amateur naturalists their approach to biological problems in the field. There is no reason why the use of scientific method should be a prerogative of professional zoologists. H. N. SOUTHERN

THE BIOLOGICAL COST OF MODERN TRANSPORT

Fred L. Soper and D. Bruce Wilson (1943). *Anopheles gambiae in Brazil* 1930–1940. 262 pp., 80 text-figures, photographs and maps. The Rockefeller Foundation, New York City, U.S.A.

The authors of this remarkable monograph, who had already much experience in the Rockefeller Foundation's dramatic campaign against yellow fever in South America, may have felt like Lord Wavell or General Alexander, when they were given the task of controlling a malaria mosquito that had already established itself and been spreading for ten years. 'Few threats to the future of the Americas have equaled that inherent in the invasion of Brazil, in 1930, by *Anopheles* (*Myzomyia*) *gambiae* Giles 1902. Only the undated arrival of another African mosquito, the vector of urban and maritime yellow fever, *Aedes* (*Stegomyia*) *aegypti* Linnaeus, can be considered to have rivaled it in importance. Warning voices (Shannon, 1930; Davis, 1931; Souza Pinto, 1931; and Soper, 1931) emphasize the tragic import of the finding of gambiae in Brazil, but no sustained effort was made to eradicate the species until amost a decade had passed.'

This mosquito, which has handsome banded legs and palpi, and dark patches among the cream-coloured scales of the wings, is one of the two most widely distributed and deadly malaria-carriers of Africa. Its ecological range is partly determined by a high preference for entering houses and there biting man, so that the larval habitat is also situated not far from human habitations. It only attacks animals in a minor degree. The larvae usually flourish only in shallow, sunny, fresh-water pools, with little or no algal growth or other vegetation, and at moderate temperatures. They are mostly absent from heavily shaded pools, fast-running streams, and dirty, alkaline or polluted waters. And (unlike, for instance, the yellow-fever mosquito) they hardly ever breed in artificial tanks or hollow trees. The eggs can stand drying for at least a week or two. When they hatch the adult may develop in a week.

The house habit of *gambiae* leads it naturally to enter and rest in those travelling houses that we call transport vehicles. In one of these the species apparently travelled from Dakar to Natal (the town on the north-east corner of Brazil, not to be confused with the other Natal in South Africa). It is believed that the passage was made in the adult stage, on a fast French destroyer, since the circumstantial evidence does not point to introduction at that period on aircraft. But in recent years it has seven times been found in aircraft reaching Natal from Dakar, and although the mosquitoes were found dead after pyrethrum spraying, some probably crossed alive. Anyhow, a flourishing colony of larvae was found near Natal in March 1930, in the irrigation ditches of some tidal flats reclaimed for hayfields.

This bridgehead, as the authors call it, was the origin of an invading army that spread some 220 miles along the coast and 200 miles inland at one point, carried virulent malaria to hundreds of thousands of people, many of whom died in spite of the use of over six million tablets of quinine and atabrin in the treatment of the sick; disrupted the economic life of a region already shattered by bad droughts; required a staff of nearly 3700 and an expenditure of over two million dollars to reduce it to extinction; and was finally wiped out to the very last mosquito by chemical control applied by brilliant and imaginative administration.

The whole of this extraordinary story developed and was finished within twelve years, and is told in an admirably succinct scientific style that does not quite suppress a lively feeling of the excitement, risk and human interest of the undertaking.

The present review is really an abstract of this story, with a few comments to set it in a wider frame of ecological happenings. The introduction of a species into a country new to it is always of great ecological interest, and we are beginning to appreciate how the history of such a dislocating force is a form of large-scale (if often unintentional) experiment from which we may hope to learn something about ecological competition. The dislocation caused by *Anopheles gambiae* in Brazil is mostly seen through its drastic effects on human health, and the natural ecological results may have been less than those arising from the spread, for instance, of the Chinese mitten crab (*Eriocheir sinensis*) into western Europe, previously reviewed here (this Journal, 5: 188–92). The special fascination for the ecologist of the present book is the interplay between human and zoological forces.

From its bridgehead at Natal, *gambiae* spread, at first rather slowly, eastwards along the northern coast of Brazil, probably helped by land, sea or river vehicles. During the first ten years no complete scientific survey was done: a bad drought in 1932 absorbed the Government's energies in this region; the Rockefeller organization had to concentrate its resources on waves of jungle yellow fever in Brazil; and an explosive outbreak in Natal itself had been so completely cleared up by mosquito control, that the dangers farther afield were not attended to. The tempo of this period is illustrated by the success of local vested interests in preventing the opening of the irrigation ditches at Natal to salt water, which, if done at the start, would have stopped the whole invasion at a negligible cost in human suffering and money.

By 1938 the *gambiae* had reached the Jaguaribe Valley from the coast, and began to spread rapidly up it. And this year and the next there was a pandemic of malaria (mainly malignant tertian, *Plasmodium falciparum*) that had an explosive violence only occasionally recorded in the annals of this disease. Practically everyone (that is, perhaps a hundred thousand people) in the affected parts of the valley had the disease, and some 20,000 died. That year only a third of the cotton crop and a fifth of the wax palm crop could be gathered in. Thousands starved, or almost so. Something had to be done. At this point the Brazilian Federal Government was galvanized into action. But 'it was recognized that an initial campaign of this type could be undertaken only by an organization free from all bureaucratic restrictions, with adequate funds and with personnel trained in a large-scale, fine-tooth comb administrative technique. Since at that time only the Yellow Fever Service possessed personnel with the necessary training, it was essential that this Service undertake the task without weighing too carefully the chances for success, but considering only the catastrophic results of failure'.

So a joint organization called the 'Malaria Service of the North-East' was set up, the strings being held in the hands of experienced men from the Rockefeller organizations. They seem to have carried through their huge task mostly by persuasion, with little reliance on force. Among the staff employed by 1940 were 49 doctors, 1090 anti-

larval inspectors, 38 microscopists and 21 statistical clerks. I do not give all these large figures to stun the reader, or glorify an astronomical way of life in ecology, but to underline one of the brilliant qualities of the American mentality.

The whole plan of campaign rested on understanding the ecology of *gambiae*. Fortunately, there was already a great deal known about this species in British Africa, which could be applied to conditions in Brazil. In one respect the situation was simpler, because domestic stock are not housed in this part of South America but wander free, so that the adult mosquitoes rested only in human dwellings. This strictly limited the breeding waters. Although the region invaded by *gambiae* is cut by the latitude of 5° S., its rainfall is less than that of East Anglia, albeit much more strongly seasonal. Because of the non-porous soil most of the rain evaporates, or stands for a while on flooded plains before evaporating. The temporary pools left after the wet season, sunken wells, seepage areas from dunes, and even hoof-prints on the edge of ponds, formed innumerable breeding places. Indeed, during four years over eleven million breeding sites were visited for inspections (not counting the enormous number controlled without inspections or mosquito counts).

Although few had thought it possible, the meticulous treatment of houses with pyrethrum sprays and of larval habitats with Paris green (an arsenical compound administered in a water-paraffin emulsion, in wet sand, or in dry dust), combined with an ingenious system of cross-checked inspection and follow-up surveys did completely extinguish the *gambiae*. 'The last autochthonous gambiae found in Brazil was collected November 9, the last larvae November 14, 1940....In spite of a year of ceaseless search, not a single native gambiae was found in Brazil during 1941.' Yet the campaign had started with 'the complete lack of a definite concrete technique which could be guaranteed to eradicate gambiae'.

The control spraying was used incidentally to take censuses of the number of adult mosquitoes in houses, either by holding a square umbrella below the place sprayed, or by picking up the insects off the floors after spraying. No detailed analysis of these counts is given here, but much of the general ecology is discussed in a separate paper by O. R. Causey, L. M. Deane & M. P. Deane (1943), *Amer. J. Trop. Med.* 23: 73–94.

The use of 260 tons of arsenical material at first caused poisoning in as many as 15·8 % of the operators, but practice and transference of susceptible workers reduced this to about 1 %. There were only six other accidents, one being an inspector who mixed Paris green in his beer to demonstrate its non-toxicity.

Campaigns such as that against *Anopheles gambiae* are seldom so successful as to cause complete eradication within a short period. The United States can record two whirlwind campaigns that were equally successful: the one against the Mediterranean fruit-fly (*Ceratitis capitata*) in Florida in 1929–30, and the earlier one against the virus of foot-and-mouth disease in California (which involved the destruction of thousands of cattle, and some 20,000 wild deer). In Britain we can instance the successful extirpation of the Canadian muskrat (*Ondatre zibethica*) from its five main British centres; and the contemporary campaign against rats bids fair to end eventually in the extinction of both species, not only in Britain but in many other parts of the world.

These are major engagements in a violent struggle against the spread of undesirable plants and animals that is affecting every country. As I have pointed out elsewhere (*Polish Science and Learning*, no. 2 (1943), pp. 7–11), we are witnessing not only the immediate dislocations caused by the introduction of various species into countries new to them, but a vast historical event—a zoological catastrophe, which is the beginning of the breaking down of Wallace's zoogeographic realms and innumerable island isolations by the activities of man, a process which will eventually reduce the rich continental faunas to a zoned world fauna consisting of the toughest species. Even a remote Subantarctic island (MacQuarie Island) can record the arrival of the European slug, *Agriolimax agrestis*, and the chickweed, *Stellaria media*!

This constant bombardment with foreign species is well illustrated by Table 18 in the *gambiae* report, which records 1503 specimens of insects and spiders from aeroplanes arriving in Brazil from Africa. There is great variety in the groups recorded (which even include the tsetse of sleeping sickness (*Glossina palpalis*)).

It is clear enough that the price of ecological stability (if one can dignify our fluctuating natural communities by this term) is eternal vigilance and a high sensitization of administrators everywhere to the ecological results of efficiency in modern transport. CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copes of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, B. M. Hobby, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Pyefinch, K. A. (1943). 'The intertidal ecology of Bardsey Island, North Wales, with special reference to the recolonization of rock surfaces, and the rock-pool environment.' J. Anim. Ecol. 12: 82–108.

The fauna, which is completely listed, does not show great diversity, owing to the exposure of much of the shore, which is rocky except for two small patches of sand. The list of the fauna, presented by transect, shows the effect of exposure in the small number of species on the exposed transects. Artificially bared rocks in different exposures were, except in the most exposed situations, first colonized by green algae, which later disappeared and were followed by fucoids. On two rocks the flora which came in was different from that of adjacent areas. In rock-pools, readings of oxygen content, *p*H, chloride content and temperature, presented in detail, show that the density of the flora is the most important factor governing oxygen content and *p*H. The fauna of the pools is listed.

Burke, F. & Williams, E. G. (1943). 'Newt larvae in brackish water.' Nature, Lond. 152: 566.

Much of the water on the west Lancashire dunes is not 'brackish' now. Newt larvae of large size were observed in water of 312 parts sodium chloride per 100,000 near Nantwich Salt Spring.

(*b*) Fresh water

Jones, J. R. E. (1943). 'The fauna of the River Teifi, West Wales.' J. Anim. Ecol. 12: 115–23.

The Teifi, one of the finest fishing rivers in Wales, with salmon, sea-trout, and trout, without coarse fish, has little or no pollution. It varies greatly in gradient, and the fauna is also rich and varied. Collections from five regions yielded about 147 species, which are listed according to abundance. As the fauna of the lower reach is virtually limited to species of flowing water (whereas that of the lower Rheidol, a stream repopulated after barrenness due to lead and zinc pollution, includes species of stagnant water) it appears that the Rheidol fauna has been partly recruited from stagnant pools.

Brown, E. S. (1943). 'A contribution towards an ecological survey of the aquatic and semi-aquatic Hemiptera-Heteroptera (water-bugs) of the British Isles Anglesey, Caernarvon and Merioneth.' Trans. Soc. Brit. Ent. 8: 169–230.

Discusses species recorded and notable absentees, describes habitats and discusses species found most commonly in each type.

Kaufmann, R. R. U. (1943). 'A contribution to the history of the aquatic Coleoptera of north and south Devonshire.' Ent. Mon. Mag. 79: 185–98; 228–30.

200 specimens of water-beetles have been recorded from Devon. A detailed list with some ecological details is given.

Popham, E. J. (1943). 'Ecological studies of the commoner species of British Corixidae.' J. Anim. Ecol. 12: 124–36.

Laboratory experiments showed that the colour acquired by a *Sigara* nymph or young adult depends on the background in which it is reared, and that pigmentation is controlled by the nervous system through the eyes. There is a high correlation between the colour of any species and that of its natural habitat. Migration is stimulated mainly by high temperature, overcrowding, or an unsuitable background. Ponds not concealed by their surroundings receive the largest numbers of Corixidae.

Walton, G. A. (1943). 'The water bugs (Rhynchota-Hemiptera) of North Somerset.' Trans. Soc. Brit. Ent. 8: 231–90.

The fresh-water habitats of north Somerset are, with few exceptions, recent, artificial and have an average *p*H of about 8. Type A has soft water, little dissolved organic matter and an acid reaction. Type B has hard water, little dissolved organic matter and is alkaline in reaction. Type C has hard water and much dissolved organic matter, and tends to have an acid reaction. Type D has hard water and a moderate amount of dissolved organic matter which appears to be derived in part from animal excreta; it tends to be alkaline in reaction. *Corixa punctata*, *C. nigrolineata* and *C. lateralis* form nearly half the total N. Somerset Corixid population inhabiting for the most part type D ponds. The Corixid population of a habitat, and to a lesser extent the other water-bugs, can be classified as (1) indigenous, (2) extraneous, due to migration mixing, and (3) adjunctive, due to the presence of some extraneous contaminating factor. North Somerset contains only 39 % of the total British Saldidae, 58 % of the British Gymnocerata, 75·5 % of the Corixidae, and all the British species of the Cryptocerata excluding the Corixidae. The only outstanding faunistic element is the presence of the subalpine *Glaenocorixa cavifrons*. Different algal floras are found in loci within a single habitat where different *Corixa* species are dominant and the diet of the *Corixa* consists of some or most of the algal flora of its optimal locus. This is suggested to be the reason why Corixidae are related to the amount of the organic matter in the subaquatic soil, as indicated by the gross relation between this and the available bases and thence the dissolved organic matter. The distribution of the four species of *Notonecta*, while primarily governed by the ovipositing habits, appears to be influenced by two other factors. *N. viridis* would appear only to be able to hold its own in slightly saline habitats, and *N. obliqua* in higher, cooler habitats. The distribution of the species of the genus *Gerris* would appear to be affected by the amount of dissolved organic matter, possibly by its relation to the surface tension. The behaviour of *Glaenocorixa* and *Cymatia* is discussed, and evidence is put forward that *Glaenocorixa* is a plankton feeder and *Cymatia* predatory. Evidence is produced to show that Corixidae migrate during October and November. It would appear that both sexes of *C. nigrolineata* and *C. lateralis* migrate together, while the females migrate more readily than the males in the case of *C. falleni* and of *C. punctata*. These insects leave their breeding places to spread to other habitats, which they again leave if unsuitable.

Reynoldson, T. B. (1941). 'The biology of the macro-fauna of a high-rate double filtration plant at Huddersfield.' J. & Proc. Inst. Sew. Purification: 109–24.

Sewage is discharged over a bed of clinkers on which a growth of bacteria and fungi forms. The main agents for removing this growth and keeping the beds aerated are larvae of the fly *Psychoda alternata*, though twelve other species of beetles, worms and spiders were also present in a low-rate (secondary) bed and ten of these were

breeding. In the high-rate bed there was only *P. alternata* and one other form breeding. By the time the effluent reached the secondary bed there was insufficient food to support a high population, and emergence of flies was on a small scale. In the primary bed too rapid multiplication of *P. alternata* can be checked by regulating the flow so that there is sufficient bacterial and fungal growth to make conditions slightly toxic.

Marshall, J. F. (1942). 'Mosquitoes in Britain.' Reprint (10 pp.) somewhat modified, with additional tables and illustrations from Biology, 8: 21–6. Issued by British Mosquito Control, Institute, Hayling Island, Hants.

Convenient summary of the general biology, and the habits of different species, which are grouped ecologically as rural (*Anopheles claviger, Aëdes annulipes, cantans, cinereus, punctor, rusticus, Theobaldia fumipennis* and *morsitans*, and ten rarer species); coastal (*Aëdes caspius* and *detritus*, and one rarer species); arboreal (*Anopheles plumbeus, Aëdes geniculatus*, and the rarer *Orthopodomyia pulchripalpis*); and domestic (*Anopheles maculipennis* —two varieties, *Theobaldia annulata, Culex pipiens* and *molestus*, and one rarer species).

Marshall, J. F. (1943). 'The control of tank-breeding mosquitoes in the City of Portsmouth.' Pamphlet (No. 33), 3 pp. British Mosquito Control Institute, Hayling Island, Hants.

An extensive search for mosquitoes in static fresh-water tanks maintained against fire hazards in the Portsmouth City area, from May to October 1942, produced 34 instances of mosquito occupation. The only species present (as previously found for most tanks in the London area) were *Culex pipiens* (which does not bite man) and *Anopheles maculipennis* (whose fresh-water races do not normally bite man). The severe biter *Theobaldia annulata* was not found in static water tanks, but was common in garden tanks of manure water in the City area. The static tanks also contained some predatory insects, including *Notonecta, Dytiscus, Acilius, Tanypus, Chaoborus* and dragonflies; also *Chironomus*. A few salt-water tanks proved to be free from two biting mosquitoes (*Aëdes detritus* and *caspius*) important locally, and known to breed mainly or entirely in salt and brackish water.

Hickin, N. E. (1943). 'Larvae of the British Trichoptera. 8 [9–10].' Proc. R. Ent. Soc. Lond. A, 18: 6–10, 11–14, 15–17, 19–21, 66–8, 69–71, 72–4, 75–7, 78–80, 81–3, 106–8, 109–11.

Describes larvae and habitat of *Limnophilus flavicornis, Anabolia nervosa, Lepidostoma hirtum, Holocentropus dubius, Limnophilus lunatus, Mystacides nigra, Limnophilus vittatus, Goera pilosa, Agapetus fuscipes, Brachycentrus subnubilus, Leptocerus aterrimus* and *Setodes argentipunctella*.

Gray, E. (1943). 'Some ecological observations upon the Infusoria.' J. R. Micr. Soc. 63: 38–42.

Some observations on microscopic fresh-water life (the term Infusoria being used in this sense) from pond, ditch, river and canal water in Yorkshire, Middlesex, Essex, Buckingham, Shropshire, Staffordshire and Warwickshire during fifteen years. Minor peculiarities of distribution are mentioned and their causes guessed at.

(c) Land

Gunton, H. C. (1943). 'Report on the phenological observations in the British Isles from December 1941 to November 1942.' Quart. J. R. Met. Soc. 69: PR1–PR32.

Again the year began, after a mild December, with a cold spell which lasted until mid-March and which included the coldest February in England and Wales since 1895. Frosts, however, were not very intense and the normal daily temperatures were reached on a few occasions. From this point until the second week in June there was a period, free from any return to harmful frosts, with three warm spells and with a dry sunny spell in the middle third, preceded and followed by rainy spells. This dry period produced a drought of 32 days—the longest for 13 years—during the greater part of which winds between north and east prevailed, mean temperatures being not far from normal with relatively warm days and cool nights. June was a dry month, cold in the middle but ending as it began with a warm spell. After the first week in July, temperature and sunshine were mainly below, and rainfall above, the normal, and although temperature rose markedly at the end of August there was no dry sunny period of any duration during that month. The period September–October produced a sequence consisting of a warm dry sunny spell, a cold wet sunless spell and a warm wet sunless ending. An initial lateness up to about day 100, amounting to 3 or 4 weeks, was due to the cold January and February. The subsequent lateness up to about day 130 was, no doubt, due to drought. With the rainy period which then ensued, responses approached the average considerably earlier than last year. With deficient sunshine in the late summer and autumn dates tended to become later again at the end of the season. The abundance of the year in respect to crops extended to cultivated and wild fruits of almost every kind, although it is not likely to be generally remembered as a genial summer owing to the frequent occurrence of weeks with deficient sunshine. The appearance of the grass fields in autumn was exceptionally green, and the weather was sufficiently quiet and free from frost to produce a wealth of autumn colours. Migrant birds were uniformly late in reaching the most northerly

zone, but the cuckoo was the only bird to be late in all three zones. It was a year of comparative scarcity of immigrant Lepidoptera, especially in the case of the painted lady butterfly, although there were arrivals in considerable numbers in a few localities. In consequence, when the single-brooded peacock butterfly had retired into hibernation, the visitors to late *Buddleia*, Michaelmas daisies, and ivy were in most places mainly confined to the second broods of small tortoiseshell and comma butterflies. Three migrants, the red admiral butterfly, silver-Y moth and the convolvulus hawk moth were recorded from the Shetlands.

Massee, A. M. (1943). 'Notes on some interesting insects observed in 1942.' Rep. E. Malling. Res. Sta. 1942: 64–8.

Notes on 22 species of insects, mites and eelworm.

Hinton, H. E. & Greenslade, R. M. (1943). 'Observations on species of Lepidoptera infesting stored products.' Entomologist, 76: 182–4.

Several hundredweight of bird guano of unknown origin first came under observation in 1937 in Kent. In 1942 the remaining hundredweight was removed to Cambridgeshire. It has been stored in a metal bin, which preserved it from the attentions of mice and birds, but allowed free access for insects. The bin was kept in an open-sided shed with no other protection from the recent severe winters. The following moths were found in it in 1943. *Endrosis sarcitrella, Hofmannophila pseudospretella, Trichophaga tapetzella, Monopis rusticella, Tinaea granella, Tinaea pellionella.* Also a single beetle larva, *Ptinus fur* and the spiders *Drassodes lapidosus, Tegeneria atrica* and *Stearodea bipunctata.* At first *Trichophaga tapetzella* was the most common species, but recently there was a great increase in numbers of *Hofmannophila pseudospretella* which now outnumbers the other species. A male *H. pseudospretella* was found mating with a female *Trichophaga tapetzella.* The spiders exercised a considerable control over the moths, catching adults and larvae. Larvae of *Tinaea pellionella* were found in and near the webs, but there was no sign of their having been attacked; no doubt the case prevents this. A key to the pupae of these common pests is given.

Ewer, R. F. (1943). 'Diurnal activity of three insect pests of stored products.' Nature, Lond. 152: 133–4.

Calandra granaria and *Ptinus tectus* were most active by night and remained hidden by day among the bags of sphaghetti. *Ephestia kühniella* was least active by night, but, though motionless, many remained exposed.

Blair, K. G. (1943). 'On the rose bedeguar gall and its inhabitants.' Ent. Mon. Mag. 79: 231–3.

Lists of Cynipids, Ichneumonoids, Chalcids and Coleoptera bred from the gall, with suggestions concerning the part that each species plays in the gall.

Williamson, K. & Rankin, M. N. & D. H. (1943). 'Field notes on the breeding of the roseate tern (*Sterna d. dougalli* Mont.).' Northw. Nat. 18: 29–32.

These observations, which differ from the Handbook (Witherby and others) on certain points, were made on an Irish colony of 243 nests within a larger ternery of other species. Single eggs or young were the most common, 36·36 % of the nests had two eggs or young, none were found with three. One ringed bird was recovered well-fledged at 19 days. The young birds were more active and hostile than those of other species and apparently had a lower mortality rate than the common and arctic terns in their vicinity. Notes on coloration of the young are included.

Bacon, A. E. E. (1943). 'Early Lepidoptera in 1943.' Entomologist, 76: 154.

Records times of day at which bee-hawk moths were seen in flight.

Johnson, E. E. (1943). 'Wainscot way.' Entomologist, 76: 211–12.

A strong flight at dusk followed by rest on the food-plant is characteristic of wainscot moths, including *Nonagria sparganii.*

Riley, N. D. (1943). 'Flight period of *Lampra fimbriata*.' Entomologist, 76: 213.

Regular flight repeated several evenings in succession, two or three moths at a time, in broad daylight a little before sunset.

Day, F. H. (1943). '*Leistus montanus* Steph. (Col., Carabidae) in Cumberland.' Ent. Mon. Mag. 79: 251.

This ground beetle has previously been recorded in Cumberland only from the summit of Skiddaw (3053 ft.). It is now recorded from the range of sandstone hills running from Penrith to near Carlisle, the elevation of which is nowhere much over 800 ft.

Wilson, G. Fox- (1943). 'The lily beetle, *Crioceris lilli* Scopoli: its distribution in Britain (Coleoptera).' Proc. R. Ent. Soc. Lond. A, 18: 85–6.

Coe, R. L. (1943). '*Callicera spinolae* Rond. (Dipt., Syrphidae) taken in Britain; its redescription, with notes on *C. aenae* Fabr. and *C. rufa* Schumm.' Entomologist, 76: 155–8.

Callicera spinolae taken on *Angelica* blossom in marches of River Deben, Suffolk, is an addition to the British list. A key to the three British species of the genus is given.

Petherbridge, F. R. & Wright, D. W. (1943). 'Further investigations on the biology and control of the carrot fly (*Psila rosae* F.).' Ann. Appl. Biol. 30: 348–58.

Contains records of emergence dates of the first and second generation, the latter being correlated with the age of the carrot crop, and notes on the movement of the flies into the fields in the cool conditions of early morning and evening.

Jones, Margaret G. (1943). 'A brown aphis, *Aphis* (*Doralis*) *cognatella*, sp.n., found on spindle tree.' Bull. Ent. Res., 34: 213–24.

Includes characters which separate it from *A. fabae* as well as short notes on its biology and alternate host plant trials. It does not colonise *Vicia faba*.

Morison, G. D. (1943). 'Notes on Thysanoptera found on flax (*Linum usitatissimum* L.) in the British Isles.' Ann. Appl. Biol. 30: 251–9.

Notes on habits of adults and larvae, place of pupation, number of generations in the year, hibernation, time of occurrence on plants, plants and objects on which found, host plants of larvae and adults, importance to flax, record of locality and collector on flax, distribution, including altitudes, in the British Isles of eighteen species.

Evans, A. C. (1943). 'Value of the *p*F scale of soil moisture for expressing the soil moisture relations of wireworms.' Nature, Lond., 152: 21–2.

Water retained in the soil pores has a pressure less than atmospheric pressure. This 'suction' is stated in terms of *p*F which is the logarithm of the height in cm. of a column of water corresponding to the suction. The cuticle of a wireworm behaves as a semi-permeable membrane and the rate of loss of water through it varies as the *p*F, not as the wetness of the soil. Thus at constant *p*F the loss of weight of wireworms is the same in sandy soil with 4 % moisture content and in rich loam with 10 %.

Taylor, E. (1943). 'A note on Dutrochet's leech, *Trocheta subviridis* Dutrochet, and its occurrence in Oxford.' Ann. Mag. Nat. Hist. 10: 431–2.

Records the discovery of two specimens of this species at a depth of about one foot in an Oxford allotment in March 1943. Records of this species in Britain are few. It feeds mainly on earthworms and may perhaps be overlooked owing to its wormlike appearance.

Miles, H. W., Henderson, V. E. & Miles, M. (1943). 'Field studies of potato-root eelworm, *Heterodera rostochiensis* Woollenweber, 1938–40.' Ann. Appl. Biol. 30:151–7.

Contains some information on influence of yield and of variety of potato on cyst production.

Boyd, A. E. W. (1943). 'Observations on the biology of the potato-root eelworm, *Heterodera schachtii* Schmidt.' Ann. Appl. Biol. 30: 157–61.

The effect of low temperature and of soil type.

Wilson, G. Fox- (1943). 'The stem and bulb eelworm, *Anguillulina dipsaci* (Kühn, 1858): the importance of collating evidence on the behaviour of biologic strains.' Ann. Appl. Biol. 30: 364–70.

Data concerning the infection of many different plants with seven biological strains of known history of the nematode are given. The technique of inducing it to infect other host plants is described in detail. The relationship that exists between flower colour in herbaceous phloxes and the degree of infection is presented.

Watson, J. M. (1943). 'Anabiosis on a soil ciliate.' Nature, Lond., 152: 693–4.

The ciliate *Balantiophorus minutus* can remain in suspended animation for periods up to three weeks in the absence of fresh water, provided it is in contact with some moisture retaining substance and that the relative humidity is high. It is thus well adapted for life in the surface soil.

(*d*) Small islands

Watson, J. S. (1943). '*Rattus rattus* on Lundy.' J. Anim. Ecol. 12: 214.

Although *Rattus rattus* was reported as rare in 1925, being replaced by *R. norvegicus*, its population is undoubtedly replenished from ships wrecked on the island, and three *R. rattus frugivorus* were caught in July 1942.

Bailey, J. H. & Britten, H. (1943). 'The Coleoptera of the Isle of Man.' Northw. Nat. 18: 73–87.

This list includes the Carabidae as far as the genus *Dromius* and is to be continued.

Rogers, H. M. (1943). 'Ornithology of the Isle of Man, 1942.' Northw. Nat. 18: 43–52.

A list of species with dates, localities and occasional notes on behaviour. Carrion and hooded crows were found interbreeding, and a few pairs of fulmars were seen on the cliffs south of Cranstal.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Williams, C. B. (1943). 'A method of collecting and storing without pressure insects and galls attached to leaves.' Proc. R. Ent. Soc. Lond. A, 18: 1–2.

In pill boxes previously separated into their three component parts.

Mosely, M. E. (1943). 'The preparation of insects for the microscope; with special reference to Trichoptera.' Entomologist, 76: 227–34, 241–51.

The three main principles upon which the method is based are (1) Parts such as the head, legs and genitalia are mounted in balsam *without* pressure. (2) One pair of wings, on the contrary, is mounted *with* pressure and dry. (3) The parts in balsam are mounted on the cover-glass and not on the slide, so that they may be as near as possible to the microscope objective.

Donisthorpe, H. (1943). 'A list of the type-species of the genera and subgenera of the Formicidae.' Ann. Mag. Nat. Hist. 10: 617–48, 649–88, 721–37.

A list bringing the type-species of the ant genera up to data to the end of 1942. The data of the type-species, its sex and type-locality are given and the name of the designator.

Benson, R. B. (1943). 'The green species of *Tenthredo* (Hymenoptera Symphyta).' Entomologist, 76: 133–44.

Keys, taxonomy and distributional records of nine British species, four of which are here brought forward as new to the British list.

Van Emden, F. I. (1943). 'Larvae of British beetles. IV. Various small families.' Ent. Mon. Mag. 79: 209–23, 259–70.

Includes keys to larvae of Cicindelidae, Trogositidae, Cleridae, Eucnemidae, Sphindidae, Meloidae, Lymexylonidae, Pyrochroidae, Lyctidae and Bostrychidae.

Collin, J. E. (1943). 'The British species of Helomyzidae (Diptera).' Ent. Mon. Mag. 79: 234–51.

Keys, taxonomic and distributional notes.

Goodey, T. (1942). 'Observations on *Mononchus tridentatus*, *M. brachyuris* and other species of the genus *Monochus*.' J. Helminth. 20: 9–24.

A detailed description of the external and internal morphology of these predatory soil nematodes.

3. PARASITES

MacNalty, A. (1943). 'Indigenous malaria in Great Britain.' Nature, Lond. 151: 440–2.

Malaria was formerly prevalent in England along the east coast where endemic foci still exist. The distribution of these foci is probably explained by the density of *Anopheles maculipennis*, the only proved native carrier. Successful measures were taken after the last war to prevent the transmission of malaria from men returning from eastern areas, but 330 cases were contracted in England in 1917–18.

Peters, B. G. & Clapham, P. A. (1942). 'Infestation with liver fluke among 73,000 cattle slaughtered in Great Britain during June, 1942.' J. Helminth. 20: 115–38.

The analysis is based on the results of a questionnaire circulated to abattoirs in Britain asking for numbers of cattle slaughtered in three weeks in June. The class, origin, and degree of fluke infestation of the cattle were to be given under special heads. The data were found to be heterogeneous in respect of all these categories and difficult to interpret.

Taking the data as a whole, the frequency of infestation was found to increase throughout June, to be lowest in S. England and in steers and highest in N.W. England and N. Wales and in cows. It was also higher among imported cattle than those bred at home. The figures are given in detail and their significance discussed. The economic loss to the meat industry is over 600 tons of liver per annum. The cattle also provide a reservoir of parasites for further infestation.

Milne, A. (1943). 'The comparison of sheep-tick populations (*Ixodes ricinus* L.).' Ann. Appl. Biol. 30: 240–50.

A detailed investigation into the two methods of comparing populations: (1) tick counts on sheep pastured on an infested grazing and (2) tick counts on a blanket dragged over the grazing.

Burtt, E. T. (1943). 'The occurrence of the tick parasite *Ixodiphagus caucurtei* du Buysson (Hymenoptera; Chalcidoidea; fam. Encyrtidae) in Great Britain.' Proc. R. Ent. Soc. Lond. A, 18: 28–9.

The distribution of this almost cosmopolitan insect is given, as well as its first recorded appearance in Great Britain (Cumberland).

Hoare, C. A. (1943). 'Biological races in parasitic Protozoa.' Biol. Rev. 18: 137–44.

Defines biological races as those subdivisions of a morphological species which are distinguishable by biological characters only. If this definition is accepted the term applies to many parasitic Protozoa now given specific rank: for example (1) to those types separated only by host specificity, e.g. trypanosomes of the *brucei* group, (2) to those producing different reactions in the same host, e.g. the Leishmanias responsible for visceral and cutaneous human disease.

These types differ in their adaptation to the chemical and physical conditions in their host, but the situation is complicated by the reactions of the host. The serological reactions have been particularly studied and some races of Protozoa, e.g. trypanosomes, seem to differ in antigenic constitution only, i.e. the ultimate difference is a chemical one.

Those races, such as the *brucei* trypanosomes, which have been closely studied for 50 years, have not altered their biological features, so it seems that their characters are hereditarily stable. It is suggested that such stable races, separable on biological criteria alone, should be given independent taxonomic status.

Nixon, G. E. J. (1943). 'A revision of the Spathiinae of the Old World.' Trans. R. Ent. Soc. Lond. 93: 173–456.

These are Braconidae which, with a single exception so far as is known, are parasitic on wood-boring beetles.

Ford, R. L. E. (1943). 'On collecting and rearing parasitic Hymenoptera with special reference to the genus *Apanteles* (Hym. Braconidae).' Proc. R. Ent. Soc. Lond. A, 18: 89–94.

4. FOOD AND FOOD HABITS

Russell, S. G. C. (1943). 'Mice eating butterflies.' Ent. Rec. 55: 122–3.

In a house a mouse ate away netting enclosing wall brown butterflies for oviposition purposes. The suggestion is made that mice might consume insects at rest on grass and low plants and be responsible for some of the depredations ascribed to birds and spiders.

Fitzgerald, B. Vesey- (1943). 'Bats taking moths at sugar.' Entomologist, 76: 173–4.

Describes use of sugared trees and lamp traps as aids for observation and capture of *Pipistrellus pipistrellus*, *Myotis mystacinus*, *M. nattereri*, *M. bechsteinii* (once in the New Forest), *M. daubentonii*, *Barbastella barbastellus*, *Rhinolophus hipposideros minutus*, and *Plecotus auritus*. *P. auritus* takes moths from sugar and moths and other insects at rest on leaves. *Myotis bechsteinii* also takes insects at rest, but hovering is not so pronounced. The others except *M. daubentonii* takes the moths as they approach the bait. This bat is strongly attracted by lamp traps. *M. mystacinus* hawks around sallow.

Hodgson, S. B. (1943). 'Bats feeding on moths at sallow.' Entomologist, 76: 147–8.

A bat, perhaps *Vespertilio pipistrellus* or *Myotis mystacinus*, hawking over a sallow bush in full bloom for about 30 min., apparently capturing moths flying near the blossoms and several times slowly fluttering among the top branches shaking them as it took insects from the catkins.

Ticehurst, C. B. (1943). 'An examination of some pellets which show an unusual diet for two short-eared owls (*Asio flammeus flammeus* (Linnaeus)).' Ibis, 85: 308–11.

Analysis of pellets collected during April in Carmarthenshire and during February in Hampshire show that one bird was living predominantly on rabbits and small passerine birds, the other on small passerines only. In the former case 5 only out of 60 pellets contained small mammal remains, although analysis of kestrel pellets showed that the area had many short-tailed field voles.

Russell, S. G. C. (1943). 'Birds attacking *Vanessa* larvae.' Ent. Rec. 55: 75.

Attacks of blackbirds, sparrows and robins on larvae of small tortoiseshell and peacock butterflies.

Hickin, N. E. (1943). 'Larvae of *Arctia caja* L., (Lep., Arctiidae) and the cuckoo.' Ent. Mon. Mag. 79: 257.

Many of these hairy larvae eaten by a male cuckoo.

Carpenter, G. D. Hale (1943). 'Birds as enemies of the larvae of *Zygaena filipendulae* L. (Lep.).' Ent. Mon. Mag. 79: 157–9.

It is difficult for birds to open burnet moth cocoons affixed to a tall grass stem above the height which it can reach by a leap from the ground. Observations show accessible ones are opened and suggest that at least some of the destruction is by young birds which are learning by 'tasting' what is, and what is not, really nice food.

Popham, E. J. (1943). 'Further experimental studies in the selective action of predators.' Proc. Zool. Soc. Lond. 112 A: 105–17.

A continuation of previous investigation into its protective value of colour varieties in the Corixid *Sigara* (*Arctocorisa*). Using *Scardinius* (*Leuciscus*) as predator, it is shown that protection is most effective in a medium sized population, and declines when it is either too small or too large. Similarly when colour varieties of prey are mixed in different populations the most abundant are taken relatively more frequently. Selection of prey for size was also demonstrated by using different species of prey. The author suggests that in the face of this demonstrable predator selection, polymorphism may be maintained by selective mating, which is confirmed by observation.

Pearce, E. J. (1943). 'Note on the feeding-habits of the genus *Bythinus* Leach (Col., Pselaphidae).' Ent. Mon. Mag. 79: 178–80.

Records of the beetle *Bythinus puncticollis* feeding on mites and *B. burrelli* feeding on a springtail.

Fraenkel, G. & Blewett, M. (1943). 'The natural foods and the food requirements of several species of stored product insects.' Trans. R. Ent. Soc. Lond. 93: 457–90.

Concerns the following beetles; *Tribolium confusum*, *Sitodrepa panicea*, *Lasioderma serricorne*, *Oryzaephilus surinamensis*, *Ptinus tectus* and *Dermestes vulpinus*: and the moths *Ephestia kühniella* and *E. elutella*.

Wiltshire, E. P. (1943). 'Substitute food-plants. (With a table of Preference-Groups.)' Ent. Rec. 55: 79–85.

Gives tables of groups of food-plant genera chosen to the exclusion of other plants by oligophagous larvae. Some species have food-plants running counter to botanical systematic affinities, and sometimes several food-plants characteristic of a particular habitat. Six examples of such ecological groups of food-plants are given.

Hodgson, S. B. (1943). 'Moths at a sugar substitute in Huntingdonshire.' Entomologist, 76: 260.

Extract of malt well thinned with methylated spirit is an excellent substitute for treacle.

5. POPULATION STUDIES

Williams, C. B. (1943). 'Area and number of species.' Nature, Lond. 152: 264–7.

There is a relationship between the number of species and the number of individuals in random samples of an ecologically uniform animal population from which α, the index of diversity, can be calculated. When α is known, it is possible to calculate the number of species to be found in a sample of any size. This reasoning can be

extended to plant communities to calculate the expected number of species in different sized areas. (Formerly, unless areas were about equal, it was difficult to compare the richness of their floras because the larger the area the more the species.) If the number of species of flowering plants is plotted against the size of areas sampled (from 1 sq. cm. up to the total surface of the earth) it is found that up to one or two acres the increase in number of species is roughly what would be expected merely from the increasing size of the sample. From here up to the size of a continent there is a much greater increase than can be attributed to the size of area sampled and which must be due to the greater lack of ecological uniformity. When the floras of the continents are added together there is a further increase in the number of species—which is a result not only of larger size of sample and ecological diversity, but of the fact that floras have evolved differently in continental isolation.

Colquhoun, M. K. & Morley, A. (1943). 'Vertical zonation in woodland bird communities.' J. Anim. Ecol. 12: 75–81.

A wood near Oxford composed of pure oak, with very sparse *Crataegus*, and a ground cover of *Pteridium* and *Rubus*, was divided into five zones: (1) upper canopy, (2) tree, (3) shrub, (4) herb, and (5) ground. Birds counted in the winter of 1941–42 were given zonal indices based on the percentage of each species in each zone and on an arbitrary figure for each zone. This index, the relative niche of occurrence, is identical with the feeding niche in the non-breeding season. The dominant species (by numbers) was different in each zone, and the greatest abundance was in the shrub zone dominated by the great tit. British oak woods may be divided into three vertical communities, the upper canopy, tree and shrub, and ground.

Southern, H. N. (1943). 'The two phases of *Stercorarius parasiticus* (Linnaeus).' Ibis, 85: 443–85.

A survey of the distribution of the light and dark-breasted phases of the arctic skua throughout its range. Data for the British Isles reveal inequalities in the general gradient in phase ratio (increase of light birds to northwards) presumably because of the small and split-up character of the populations. Mating was at random in one sample, but in another like birds tended to pair with like.

Fisher, J. & Vevers, H. G. (1943). 'The breeding distribution, history and population of the North Atlantic gannet (*Sula bassana*). Part 1. A history of the gannet's colonies, and census in 1939.' J. Anim. Ecol. 12: 173–213.

In 1939, within one breeding season, a census in which 27 experienced observers took part, was made of all the gannet breeding colonies in the world except a small number containing about 2·5 % of the world population. The 22 breeding colonies, of which 13 were in Britain and the Faroes, 3 in Iceland, and 6 in the Gulf of St Lawrence, contained 165,600 ±9,500 breeding individuals. As a basis for the history of each of 39 places where gannets have bred, or are suspected of having bred, no less than 251 citations to the literature are given, besides 45 persons listed as supplying information. There are many references to killing mature and young birds and taking eggs, practices now mostly stopped. The account is illustrated by fine photographs of many gannet rocks and islands, many of them aerial ones taken by R.A.F. Coastal Command; and a map of the gannet colonies in the North Atlantic.

Winser, M. P. & King, J. M. B. (1943). 'Census of swallows and house-martins in the Sedbergh district, N.W. Yorkshire.' Brit. Birds, 37: 32–4.

Censuses were caried out on 4250 acres of pasture in 1938 and 1942. Swallows remained constant in this period (17·2 and 15·0 pairs per 1000 acres), while house-martins increased (6·5 and 13·6 pairs per 1000 acres).

Thompson, C. & Thompson, D. Nethersole (1943). 'Nest-site selection by birds.' Brit. Birds, 37: 70–4, 88–94, 108–13.

A compilation, from personal notes and literature, on the shares of the sexes and methods adopted by them during this phase of the breeding cycle.

Ryves, B. H. (1943). 'An examination of incubation in its wider aspects based on observation in North Cornwall.' Brit. Birds, 37: 42–9.

Contains intensive observations on several little-known phases of reproduction on various species. Notes are given to show that the interval between nest building and laying may be much longer at the beginning of the breeding season, and also that the rapidity of re-nesting varies with the stage at which the first nest was destroyed. Similarly a third brood usually requires a longer interval than the second. Other observations also show great variation in the exact time of commencement of real incubation contrasted with casual brooding.

Höhn, E. O. (1943). 'Some observations on the common pochard.' Brit. Birds, 37: 102–7.

A description of the social nature of courtship in *Aythya ferina*, which takes place some time before pairing. Also contains data on breeding biology.

Bullough, W. S. (1943). 'Autumn sexual behaviour and the resident habit of many British birds.' Nature, Lond., 151: 531.

Birds which migrate in the autumn do so apparently because the sexual impulse disappears and with it their attachment to nesting sites and territories. Those which have lost the migratory impulse (such as the British race of starlings) show some sexual display throughout the year, probably because of the autumn activity of that part of the anterior pituitary gland causing hormone secretion.

Went, A. E. J. (1943). 'Salmon of the River Shannon. I. An analysis of the incoming populations of 1941. II. Changes in the character of the stocks since the year 1929.' Proc. R. Irish Acad. B, 49: 151–75.

Since the construction of the new hydroelectric dam there has been a change in the incoming fish of 1941 compared with those of 1927 and 1928. In 1941 the average age of smolts was higher; grilse formed three-quarters of the total run instead of one-quarter to one-third and consequently the average weight of the catch was lower. About 70 % of the catch was made both in June 1941 and 1942 compared with 21–27 % in each of the months April to June 1927 and 1928.

Houghton, A. T. R. (1943). 'Development of the Ribble Problem: some comments on increasing salmon runs.' Salm. Trout Mag. Lond. No. 107: 36–41.

The number of salmon caught in the Ribble has risen fairly regularly from 552 fish in 1931 to 3263 in 1941. The factors which may be responsible for this increase are discussed. They include re-stocking, abatement of pollution and more efficient protection of the spawning stock, but no conclusion as to the relative effects are drawn.

Gardiner, A. C. (1943). 'Phosphorus and fish: some observations on the phosphorus content of natural waters.' Salm. Trout Mag. Lond. No. 107: 45–55.

A discussion of the variations in phosphate content of natural waters in relation to living organisms and the carbonate-carbon dioxide system, with particular reference to its bearing on the total productivity of fresh water.

Frost, W. E. (1943). 'The natural history of the minnow, *Phoxinus phoxinus*.' J. Anim. Ecol. 12: 139–62.

Bi-monthly collections from December 1939 to November 1941 in Lake Windermere yielded 2,600 minnows and from May 1940 to April 1942 in the River Brathay, an affluent, yielded 1800. Minnows are active in shallow water from April to October, and hide under stones in deeper water, though not without feeding, from November to March. Length frequency curves, supported by scale examinations, show three year-classes and possibly four. The mean length in Windermere at the end of the first year is 33·7 mm., second year 56·2, and third year 68·8. The very detailed study of food included 1228 fish from Windermere and 833 from the River Brathay. Gut contents were divided into 18 kinds of food, which are presented in tables and graphs as percentages for each of the two years, for each month, by seasons, and also as surface, mid-winter, and bottom food. Further, the food of 50 trout fry is given for comparison. The main food in Windermere is Cladocera, in the River Brathay filamentous lagae. A few minnows are sexually mature at the end of the first year, and the majority in the second year.

Barnes, H. F. (1943). 'Studies of fluctuations in insect populations. X. Prolonged larval life and delayed subsequent emergence of the adult gall midge.' J. Anim. Ecol. 12: 137–8.

Contarinia tritici can emerge the same summer (late August), the next spring, and two winters after its larvae attack the wheat. Its parasites generally emerge after the first winter. *Sitidoplosis mosellana* emerges up to four years, but not in the same summer. Its parasites survive two winters in the soil. This variability protects the race and is a cause of sudden increases in numbers.

Tomlinson, T. G. (1943). 'Biological control of the fly population in sewage filters'. Nature, Lond. 152: 52.

The fly *Anisopus fenestralis* completes its life cycle in 121 days at 9° C. and in 39 days at 21° C. and is a nuisance in houses near filter beds. Another fly, *Psychoda alternata* also lives in sewage filters but is not much nuisance. *Anisopus* develops throughout the year, but its emergence can be prevented in the spring if there is sufficient accumulation of solid matter in the upper layers of a filter. Development of *Psychoda* is restricted to the summer when it successfully competes with *Anisopus* thereby keeping its numbers down.

Lloyd, Ll. (1943). 'Materials for a study in animal competition. Part III. The seasonal rhythm of *Psychoda alternata* Say and an effect of intraspecific competition.' Ann. Appl. Biol. 30: 358–64.

The periods of peak output found in the seasonal trend of *Psychoda alternata* are explained by the theory that there are two successions of generations running persistently and alternating with one another. When the cycles are rapid an intraspecific competition is set up.

Bird, J. F. (1943). 'Apparent sex disparity in Lepidoptera.' Entomologist, 76: 260–1.

Records breeding a series of males, but only two females, from ova of *Hamearis lucina* (Duke of Burgundy Fritillary butterfly). Gives lists of species showing a preponderance of females when obtained in the imaginal state and species showing such preponderance even when bred.

Purefoy, E. B. (1943). '*Polygonia c-album* near Maidstone.' Entomologist, 76: 226.

A comma butterfly observed ovipositing. Thin and poor plants were selected and thick bunches of hop leaves avoided. All eggs taken home were successfully bred, those left hatched and the larvae fed, but none survived. They generally disappeared during the night and it was believed that they were devoured by snails.

Kettlewell, H. B. D. (1943). 'A survey of the insect *Panaxia* (*Callimorpha*) *dominula*, L.' Proc. S. Lond. Ent. Nat. Hist. Soc. 1942–43 (1): 1–49.

Small colonies of the scarlet tiger moth exist close to others, but pairing between them need seldom if ever take place owing to the habits of the imagines and the date of emergence which is very much affected by immediate environment. Mutations in this species tend, therefore, to be localized. This paper considers all available information concerning habitat, life history, parasites, fertility, genetics, related species and sub-species, variation and British and Continental distribution. Two of the five plates are in colour.

De Worms, C. G. M. (1943). '*Nymphalis polychloros* in the New Forest.' Entomologist, 76: 147.

Record of a large tortoiseshell butterfly seen on March 21st, 1943. It is 20 years since this insect was at áll plentiful in the Forest, but it has recently shown a great increase in numbers in the Eastern counties and may be returning.

Wheeler, L. R. (1943). '*Nymphalis polychloros*.' Ent. Rec. 55: 111.

The large tortoiseshell butterfly appears to be on the increase in the Seaford district.

Taylor, E. (1943). 'Abundance of *Tettigonia viridissima* L. (Orthopt.) in N. Berks.' Ent. Mon. Mag. 79: 208.

Large numbers of the great green grasshopper were observed in a field of rye in N. Berkshire. A dozen or more could be seen at any one time and, although the species occurs regularly in the locality, never has it been so plentiful in the last 14 years.

Donisthorpe, H. (1943). 'Swarming of *Sepsis cynipsea* L. (Dipt., Sepsidae).' Ent. Mon. Mag. 79: 184.

Millions of specimens swarming in the evening in Windsor Forest.

Scott, H. (1943). 'Swarming of *Psectrosciara tenuicauda* Duda (Dipt., Scatopsidae).' Ent. Mon. Mag. 79: 156–7.

Several hundred specimens of this small fly swarming round the top of a house at Henley, Oxfordshire, 18 May 1943.

Boyd, A. E. W. (1943). 'Stimulation of larval emergence in *Heterodera schachtii* Schmidt, by certain concentrations of silver compounds.' Ann. Appl. Biol. 30: 161–3.

It is concluded that many more eggs in *H. schachtii* cysts are mature and capable of hatching than can be accounted for by ordinary larval liberation brought about by means of root excretion alone.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Thomson, A. Landsborough (1943). 'The migration of the sandwich tern. Results of British ringing.' Brit. Birds, 37: 62–9.

Ringing returns of *Sterna sandvicensis* from British colonies show a dispersal of young birds before migration, some even travelling 300–400 miles north of where they were bred. Real migration starts in September and young birds have generally travelled down the coast of Africa to south tropical latitudes by winter. Older birds may winter round the south of Africa and up to Natal. Many birds, both old and young, remain in these latitudes during their breeding season.

Flynn, J. E. (1943). 'Hibernation versus migration.' Entomologist, 76: 190–91.

Favours view that worn butterflies have hibernated, fresh ones have migrated.

Eliot, N. (1943). 'Migration v. hibernation.' Entomologist, 76: 193–8.

Considers migration and hibernation as mutually exclusive imaginal characteristics. Weakness or failure of the migratory instinct may cause individuals to remain in unsuitable latitudes, and in such cases a few may successfully overwinter provided the climatic conditions happen to be favourable.

Allan, P. B. M. (1943). 'The travel of larvae.' Entomologist, 76: 159–64.

A discursive discussion of the distance which a larva travels between its food-plant and its pupation site.

Harrison, J. W. H. (1943). 'Immigrant Lepidoptera in the Inner and Outer Hebrides.' Ent. Rec. 55: 108–9.

Records of painted lady, red admiral, and large white butterflies, silver-Y, humming-bird hawk and rush moths.

Sherlock, R. J. (1943). '*Papilio machaon* in Devon.' Entomologist, 76: 207.

A male captured in August on the cliffs about a mile east of Sidmouth.

Jary, S. G. (1943). '*Papilio machaon* L. (Lep.) in Kent.' Ent. Mon. Mag. 79: 255.

Records of one adult in flight near New Romney and a number of larvae found upon carrot foliage near Canterbury and Ashford.

Pilleau, N. C. E. (1943). '*Papilio machaon* at Littlehampton.' Entomologist, 76: 234.

A large specimen seen in a clover field, 12 August 1943.

Somerset, W. H. B. (1943). '*Colias croceus* Fourc. (Lep., Pieridae) in Hants.' Ent. Mon. Mag. 79: 279.

See also notes by **L. S. V. Venables, A. H. Hamm, B.M. H[obby], H. G. C[hampion] (1943).** Ent. Mon. Mag. 79: 279–80.

The clouded yellow butterfly appears to have been more abundant in the neighbourhood of Oxford during 1943 than in any of the previous three years, and to have been frequently seen in the gardens of more or less built-up areas.

Richards, A. W. (1943). 'Extension of habitat of *Pararge aegeria* in N. Hampshire.' Entomologist, 76: 224.

In 1924 the speckled wood butterfly occurred but sparingly in Alice Holt and Wolmer Forest, N. Hampshire. It was not found elsewhere locally until 1932 when a few occurred on the Hog's Back. During the last six years it has occupied nearly all the smaller woods in the district and is apparently still extending its range.

Henderson, J. (1943). '*Pararge aegeria* in Argyllshire.' Entomologist, 76: 253.

Author has not heard of the occurrence of the speckled wood butterfly so far north before.

Bird, J. F. (1943). '*Celerio livornica* and *Heliothis peltigera* at Clevedon.' Ent. Rec. 55: 76–7.

Twelve striped hawk moths taken between 30 May and 9 June, and two bordered straw moths on 10 and 11 June 1943. All visiting valerian.

Lees, F. H. (1943). '*Celerio livornica* in S. Devon.' Entomologist, 76: 170.

Sixteen striped hawk moths taken between 5 and 13 June in the evening at valerian.

See also notes by **Cruttwell, G. H. W., Sale, G. H., Holmes, J. W. O., Temple, V., de Worms, C. G. M., Lipscomb, C. G., Harbottle, A. H. H., Featherstone, P., Brasnett, G., Crow, P. N., Lowther, R. C., Cowin, W. S., Williamson, K., Sangster, D., Harper, G. W., Carr, F. M. B., Jones, W. Stephen-, Simes, J. A. (1943).** Entomologist, 76: 189–90, 207, 238, 259.

Lowther, R. C. (1943). '*Herse convolvuli* in Lancashire.' Entomologist, 76: 238.

Two convolvulus hawk moths seen in September at tobacco blossom.

See also **Tait, C. H., Taylor, E., Fry, R. O. J., Kevan, D. K., Harbottle, A. H. H., Foster, A. H. (1943).** Entomologist, 76: 238, 251, 257–8.

Cockayne, E. A. (1943). '*Sidemia zollikoferi*, Freyer.' Ent. Rec. 55: 88–9.

A specimen of this immigrant Russian moth taken at Leeds in August, 1939, brings the total number of examples recorded in Britain to 13.

Coe, R. L. (1943). '*Drosophila repleta* Wollaston (Dipt., Drosophilidae) new to Britain, with notes on the species and some account of its breeding-habits.' Ent. Mon. Mag. 79: 204–7.

This fly was originally described from Madeira, but is now known to occur in the Palaearctic, Nearctic (up to 46° 14′ N. lat.), Neotropical, Ethiopian, Oriental and (doubtfully) the Australasian Regions. It is evidently an introduced species both in the U.S.A. and in England and is probably of tropical origin. Since 1942 it has occurred in various London canteens and has been found breeding in rotting onions lying in a basement kitchen.

Hinton, H. E. (1943). 'Notes on two species of *Attagenus* (Col., Dermestidae) recently introduced into Britain.' Ent. Mon. Mag. 79: 224–7.

Until now only three species of the beetles *Attagenus* have been recorded in Britain, viz. *A. pellio*, *A. trifasciatus* and *A. piceus*. *A. trifasciatus* is a native of southern Europe and has not been found for more than a hundred years in Britain. *A. piceus* is nearly cosmopolitan, a serious pest of stored products, and now established in Britain. *A. gloriosae* and *A. alfierii* both already known in other countries as pests of stored products, have recently been introduced into Britain. Description and keys to adults and to three species of larvae are given.

Hinton, H. E. (1943). 'A key to the species of *Carpophilus* (Col., Dermestidae) that have been found in Britain, with notes on some species recently introduced with stored food.' Ent. Mon. Mag. 79: 275–7.

Nine species of *Carpophilus* have been found in Britain, and all have apparently been introduced with stored food products. Of these, six have been recorded since 1900 when only *C. hemipterus*, *C. dimidiatus* and *C. sexpustulatus* were on the British list. *C. hemipterus*, *C. dimidiatus*, *C. sexpustulatus*, *C. ligneus*, *C. marginellus* and probably *C. obsoletus* can now be considered to be established in Britain. *C. flavipes* has been found in this country on only one occasion and must be regarded as an accidental introduction. Two additional species, *C. humeralis* and *C. maculatus*, are here recorded for the first time in Britain, and of these it is possible that *C. maculatus* may become established.

Champion, H. G. (1943). 'An indoor swarm of *Pteromalus deplanatus* Nees (Hym., Chalcidoidea, Pteromalidae).' Ent. Mon. Mag. 79: 259.

This insect, a parasite of the green oak moth *Tortrix viridana*, is well known to swarm in buildings, finding its way into closed spaces, even those apparently almost completely sealed. An instance is given of 118 specimens being found inside a picture frame hanging on a wall! The house was surrounded by a screen of conifers and fruit trees and there was no oak within sight or within 400 yards.

7. REPORTS OF ORGANIZATIONS

British Trust for Ornithology (1942). Ninth Report (Summer 1943). 16 pp.

Contains summaries of progress in various inquiries, the results of which will be noticed as published. Mention should be made of the collection of aerial photographs of bird rocks and islands, mostly on the west coasts of Britain, which the Trust is gathering with the co-operation of R.A.F. Coastal Command.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1943

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and *less* Payments in advance:						
Members taking *Journal of Ecology* only	217	10	0			
Members taking *Journal of Animal Ecology* only ...	127	7	3			
Members taking both Journals	96	15	0			
				441	12	3
Interest on Investments	55	2	1			
Interest on Deposit Account	2	2	11			
				57	5	0
Journal of Ecology. Sales less Cost				76	9	1
Index to *Journal of Ecology*, vols. I–XX, Sales ...	3	16	0			
Less Expenses	3	7	6			
					8	6
				575	14	10
Balance—Deficit for the Year (To Balance Sheet) ...				12	13	11
				£588	8	9
Journal of Ecology, 1943:						
Sales: Current vol. 31				441	14	0
Back volumes and parts				133	13	9
				£575	7	9
Journal of Animal Ecology, 1943:						
Sales: Current vol. 12				211	13	2
Back volumes and parts				50	8	4
Reprints of papers				10	15	6
				272	17	0
Balance (see above, under Expenditure)				405	0	7
				£677	17	7

Expenditure

	£	s.	d	£	s.	d.
Working Expenses:						
Printing and Stationery	3	5	10			
Postages	11	15	9			
Travelling	13	9	11			
Committee on Nature Reserves	43	7	2			
Meeting Expenses	17	12	0			
Audit Fee	3	3	0			
Bank Charges		10	5			
Clerical assistance	15	0	0			
				108	4	1
Grant: to Freshwater Biological Association ...				10	0	0
Biological Flora of the British Isles:						
Cost of Printing	80	7	11			
Less Sales	15	3	10			
				65	4	1
Journal of Animal Ecology. Cost *less* Sales				405	0	7
				£588	8	9
Journal of Ecology, 1943:						
Costs: Paper, Blocks, Printing and Binding ...				386	18	10
Publishers' Commission				82	11	9
Carriage, etc.				16	7	1
Insurance of Stock				6	10	0
Editorial expenses				6	11	0
				498	18	8
Balance (see above, under Income) ...				76	9	1
				£575	7	9
Journal of Animal Ecology, 1943:						
Costs: Paper, Blocks, Printing and Binding ...				602	14	1
Publishers' Commission				43	6	2
Carriage, etc.				10	19	8
Insurance of Stock				10	7	2
Fee for checking references				10	0	0
Special notice					10	6
				£677	17	7

BALANCE SHEET AT 31 DECEMBER 1943

Assets

	£	s.	d.	£	s.	d.
Cash at Bank: Current Account	158	18	0			
Deposit Account	350	0	0			
				508	18	0
Publishing Accounts—Amounts due from Cambridge University Press:						
Journal of Ecology. Balance of Account	272	16	5			
Journal of Animal Ecology. Balance of Account	106	19	6			
Journal of Ecology. Index Volume		8	6			
Biological Flora of the British Isles	12	3	3			
				392	7	8
Investments at Cost:						
Held 31 December 1942—						
£1,200 of 3½ % War Loan	1,230	4	1			
£200 of 5 % Conversion Loan	198	10	0			
Purchased 28 April 1943—						
£300 of 3 % Savings Bonds	300	0	0			
				1,728	14	1
				£2,629	19	9

A further Asset, not valued, is the Unsold Stock of Journals and Index Volume held by the Publisher for the Society.

VICTOR S. SUMMERHAYES,
ALEX. S. WATT.
Hon. Treasurers.

Liabilities

	£	s.	d.	£	s.	d.
Members' Subscriptions, prepaid for 1944				9	15	0
Library Fund				1	5	0
Grant from F. L. Vanderplank for *Journal of Animal Ecology*				5	0	0
Printing Accounts due to the Cambridge University Press:						
Journal of Ecology, vol. 31, no. 2 and Reprints	229	19	9			
Journal of Animal Ecology, vol. 12, no. 2 and Reprints	392	2	10			
				622	2	7
Sundry Accounts due:						
Nature Conservation Report (two Accounts)	31	2	6			
Expenses of Special Meeting	2	5	0			
				33	7	6
General Revenue Account:						
Surplus in hand 31 December 1942	1,971	3	7			
Less Deficit for 1943	12	13	11			
				1,958	9	8
				£2,629	19	9

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 Bishopsgate, E.C. 2
and
231*a* High Road, Loughton, Essex.
9 *May* 1944.